A STUDY OF THE VASCULAR SUPPLY TO THE CARPELS IN THE FOLLICLE BEARING RANUNCULACEAE.

by

MABEL S. FRASER.

CONTENTS.

HISTORICAL INTRODUCTION

It was in 1790, that Goethe (126) published his doctrine of metamorphosis. Prior to that date, only two authors had expressed any fundamental ideas with regard to the nature of the flowers. Wolff (120) in his "Theoria Generationis" published in 1759, expressed the view that the whole plant consisted of nothing but stem and leaf, the root being a modification of the former. The floral appendages were appendicular organs. The production of floral leaves was the result of a degeneration in the quality of the sap, the richest portion being used up at a lower level by the first formed vigorous foliage leaves.

The following year Linnaeas (59) published his "Prolepsis." He also expressed the same idea as Wolff, that all the floral organs were leaves. He partly based his evidence on teratological specimens, in which the various organs were sometimes found to be replaced by leaves. He further considered the flower to be a modified shoot, in which the growth of five years was compressed into a single year. Believing that the different floral whorls were developed the one from the other, and observing that they encircled each other, he attributed the various floral envelopes to different tissues of the stem. The bark gave rise to

the calyx, the phloem to the petals, the wood to the stamens, whilst the carpels arose from the pith.

Although other papers had been published thirty years before Goethe published his views, yet he appeared to be unaware of their existence. It is to him that we turn for the first definite theory on the relation of the floral parts to the vegetative parts. From a study of the life cycle of annual plants, he stated that the vital powers were expressed in two ways - ~~pithy~~ firstly growth and secondary reproduction. As a plant grows there is a series of progressive developments of a successive nature. First of all, there are the seed leaves, following these, there are the first leaves, which frequently differ in size and shape from the adult foliage. Then comes a time when the flower appears. The stem leaves become gradually smaller, and simpler, but increase in width at their base to form the calyx. Nature forms no new organ - the calyx is the result of modification and union of the leaves.

During reproduction all the parts become contracted, and aredeveloped in close proximity. But in the flower, the whole is constituted of modified leaves. "Whether a plant produces leaf buds, flowers, or fruit, it is still the self same organ, though

performing different offices and disguised under different forms." Within the flower, there is an alternation of contraction and expansion in the different whorls - contraction in the calyx, expansion in the petals, contraction extends to the stamens and carpels, with expansion again in the fruit.

Metamorphosis is the operation by which one and the same organ presents itself under various disguises. Goethe postulated three types of changes - regular, irregular and accidental, the first of which is of importance to us. Throughout his work, the word "metamorphosis" is used in two senses, the first interpretation being an actual change in the organs, arising from a transmutation of the species, the second an ideal meaning - cotyledons, foliage leaves and the floral organs originate on the stem and are included under the general term "leaf." The metamorphosis of the later botanists has been one of ideal transformation.

This theory propounded by Goethe received support from numerous other botanists of the time. Following this work, interest was centred particularly on the gynoecium. One school of thought, supported

later by Payer, considered that the wall of the carpel was an appendicular structure, while the placentae were axile in origin. The other school of thought considered that the whole carpellary structure was appendicular.

Van Tieghem (99) in his famous paper, published in 1867, finally, from anatomical evidence mainly, showed that the whole of the gynoecium was an appendicular structure. First of all, he laid down laws for the recognition of an axial structure and an appendage - laws which are of a truly fundamental character. In his study he considers teratology, development, morphology and anatomy. He rejects, or uses with caution, the teratological specimens, for even after careful consideration the results are doubtful. The study of development determines the order of appearance of the various whorls, but this does not show whether a structure belongs to the stem or is an appendage. To him only anatomy can determine the nature of an organ, axile or appendicular, and can show the exact form of departure of a trace. Using anatomy he investigated a tremendous number of flowers, consisting of a varying number of parts, with carpels

free or fused, and inferior or superior ovary.

His conclusion was that, no matter the type of carpel, or the placentation, the whole is appendicular and is a leaf like organ, producing ovules on its borders. Even if the stem be prolonged above the level of insertion of the carpels, it never produces ovules.

Numerous contributions were added, many from teratological specimens, which bore out Goethe's theory. This remained unattacked until the beginning of this present century. By this time Darwin had published his "Origin of species," and Hofmeister in his "Vergleichende Untersuchungen" had made known the detailed life histories of Liverworts, Mosses, Ferns, Gymnosperms, Fossil records of past ages, had brought to light new types, which had existed in earlier epochs, and from which it was possible to derive some of our present day types.

It was in 1908 that Bower (15) brought forward his "Strobidoid Theory," which is, of course, directly opposed to Goethe's theory of progressive metamorphosis. To Bower the converse of Goethe's theory is the more probable situation, i.e. the foliage leaf is a

sterilised sporophyll. These considerations of Bowers were made previous to the discovery by Kidston and Lang of the Psilophytales.

The next attack on the carpel was lodged by Saunders in 1923 - the carpel polymorphism theory (75). In the majority of plants, according to this theory, the carpel, as we know it, is not a single structure, but it is made up of a varying number of carpels, frequently two, but in other types the number varies, up to 20 in the Papaveraceae.

Saunders has established three types of carpels - the valve, the semi-solid or pseudo-valve and the solid carpel. The foundation of each of these is the vascular bundle. The valve carpel is described as retaining the typical leaf form with a conspicuous midrib. Reticulate venation of the pinnate type is usual, but there may be an approach to the palmate form, as in Coptis asplenifolia. The solid carpel, which has been evolved from the valve type, may only be represented by a vascular bundle. It may, however, be surrounded by ground tissue, and the actual margins of the carpel, in some cases, are visible! This type of carpel is found associated with either of the other two types. If associated with a true valve carpel, it

is the solid carpel which is fertile and bears the ovules. The semi-solid type is not very strictly defined, and appears to combine character of both groups. Described as outwardly of a valve contour, it differs from the true valve carpel, having the placentae displaced from the contact edges of the carpels, to a position on either side of the centre line. In this carpel there is a double central strand (the midrib) from which connections run out to the ovules, and branches pass out to supply the ovary wall. The venation is such that the carpel can split between the centre of the two bundles. This type of carpel may be found associated with either of the other two types, and it would appear that they are always fertile.

The first type studied was the Cruciferae, and in this she found four carpels present - two valve carpels and two solid carpels. From this she proceeded to investigate numerous other types and applied to them the result of her investigation of the Cruciferae. Thus she has found that the valve, semi-solid and solid type of carpel are found to occur in the majority of the families of flowering plants and that it is the exception for a carpel to be of a truly

monocarpellary structure.

In the application of her theory she claims to be able to overcome all the difficulties inherent in the old theory of the metamorphosed leaf. Her explanations are frequently long and complicated. She is inconsistent in her interpretations, and on attempting to apply her theory to results of observations, one is at a loss to know exactly how the originator of the theory would interpret the results. Throughout her work, it would appear that two similar conditions are often interpreted in two different ways.

This work called forth various criticisms, of which those of Eames (27) may be mentioned. The author of the theory fails to take into account the known facts of anatomy, either of stem or leaf. The effect of cohesion upon the vascular system is not taken into account. Stelar bundles are interpreted as carpellary traces. He criticises separately such statements of fact as "In the gynoecium every trace determines a carpel," "Traces to two organs cannot arise in one," "Traces to one organ cannot arise on opposite sides of the receptacle." The supply to a carpel, as interpreted by Eames, is fundamentally

similar to that of a leaf, whilst the receptacle represents the axis. He points out Saunder's failure to realise the effect adnation and cohesion must have had upon the vascular supply. He demonstrates all the points from widely separate groups in the plant kingdom.

Thomas (182) in 1931, after studying the carpel venation in a few Ranunculaceous and Rosaceous genera, and with the knowledge of the primitive Augiosperm Gristhorpia, puts forward a new theory with regard to the nature of the carpel, indicating how the modern carpel may have been derived from such a type of fossil.

First of all, he forces himself from any preconceived ideas, such as Goethe's theory and its corollaries. The stamens and carpels are microsporophylls and megasporophylls. The fact that stamens may bear ovules and the carpels give rise to anthers and pollen sacs suggests to Thomas that the two types of sporophylls were originally homologous and similar structures. Teratological specimens, in which a carpel becomes leaf like, have been produced by crossing experiments, so that this new type of structure may be a result of the rearrangement of genes.

Starting with a young sporophyll of Gristhorpia, his first postulate is the reduction of the ovaries to a single pair, and following this there is fusion of the two fertile ovaries. On contact it was impossible for the ovary wall to curve round, and thus instead of two ovaries, there is present a single structure with an apical stigma and two rows of ovules. Involved in this process was the axis. On this "New Morphology" the ovules are held to represent original terminal structures, the placentae separate branches, and the carpellary wall a cupular structure.

This theory presents a new morphological concept, and involves, if carried to a logical conclusion, a complete re-adjustment of our ideas regarding the primitive Angiosperm flower. With this theory as a starting point the primitive flower would have a solitary carpel, terminating the apex of the receptacle. The origin of the hemaphrodite flower, and the accompanying calyx and corolla, are problems which have not appeared to confront the founder of this theory, not to mention the flowers with a greater number of parts in each whorl. But in his later paper, as a type exhibiting a primitive stigma, he immediately turns to the Drimys species - in which

there are present a large number of parts.

In a paper published later (104) Thomas still adheres to his original idea as regards the nature of the carpel stated above, but modifies his idea with regard to the nature of the origin of the stigma. To him there are three ways in which the stigma may have arisen. (1) That the appearance of glandular structures at the apex of the fertile leaf was the first step towards the closure of the carpel. (2) That the leaf margins would be inrolled previous to the evolution of pollination through the medium of a stigma, and (3) That the closure of the leaf was preceded by the development of a marginal band of secretary cells. This third interpretation is the one which is considered the most probable, despite the fact that it is opposed to the work of Grégoire. Believing that the origin of the stigma is closely related to the Angiospermous habit, an intensive study has been made of the literature relating to the stigma and transmitting tissue, and a few examples of primitive types have been studied, in the Rosaceae and Magnoliaceae particularly. From this he concluded that the stigma appears to be a modified portion of the inner surface of the ovary wall; but this did not include a developmental study of the transmitting

tissue and stigma. Based on a study of various species of Drimys and Alchemilla it is postulated that the earliest stigmas arose near the lower part of the ventral side of the ovaries. This represents, together with the transmitting tissue, the marginal parts of the inner surface of the cupules of Gristhorpia, which was lined with glandular hairs.

This theory of the origin of the carpel and stigma he believes to explain the different forms of stigmas, accounts for the transmitting tissue, is in accord with our knowledge of ontogeny, despite the fact that it is opposed to Grégoire's results, and also accounts for the main features of the vascular supply.

He invited criticism of this new theory, and his challenge has been taken up by Thompson (108), who adversely criticises the theory and later states his own views of the subject of the Angiospermous carpel (109). The opening quotation from Schleiden is very pertinent - " A man has scientific judgment only on such objects as he is acquainted with through his own researches; how many may there be who have never once attempted to form an independent opinion of the nature of the organs of propagation of plants by

the investigation of their development on only one single plant." The Caytoniales are the group on which Thomas bases his speculations. Their qualifications, in Thompson's estimation as a basis are - they possess cupule like envelopes for their seeds, are diesociated in any sense from microspore organs, and that their affinity is unknown.

Like Thomas he frees himself from old morphological ideas - but goes a step further. To him there is no valid basis for the belief in an evolution of carpels to bear and protect the ovules, or for the pollen to be received by the stigma. The flower is essentially a sporogenous axis, potentially heterosporous, excepting the base, where the bracts and sepals are produced. Towards the base of this axis, the tissue is essentially potential microsporangium. The lower emergences of this portion of the receptacle are sterile, and take the form of staminodes or petals. The upper of this part is diverted from its original function of spore bearing, and these emergences become the styles of carpels. The remaining tissue of the axis is megasporangial. The placentae are favoured tracts of tissue of the megasporangium, and on this nucellar formation takes place.

The difference between a flower possessing an inferior and a superior ovary lies entirely in the development of the spore bearing axis, the difference depending upon the part played by apical and toral growth. Thus he does not consider either the flower with the superior ovary as primitive, or that of the inferior ovary as advanced. Neither is derived from the other, but are different expressions of the limitations of apical growth of a heterosporous axis.

Thus the "modern" theories on the carpel are a return to theories expressed a long time ago, before our present day high standard of technique was invented. That of Thomas returns to the school of thought prevalent before the work of Van Tieghem, and Thompson returns to a view not far removed from that expressed by Schleiden. (93).

GENERAL INTRODUCTION

From this brief historical sketch, it will be seen that the carpel of the Angiosperm flower has been the subject of many papers, and much discussion. It was felt that some of the theories discussed had been advanced without sufficient attention being paid to the study of the relation of the carpellary whorl, to the other whorls. Also that this work had been carried out, on what the majority of botanists consider to be highly evolved families, and that much valuable imformation might be obtained from a detailed study of more primitive types.

The most primitive type of carpel is usually considered to be the follicle. This immediately suggested such families as Ranunculaceæ and Rosaceæ, and it was decided to concentrate upon the former. This offers a wide range of type, as regards the arrangement of the floral organ, and also the number of parts in each whorl. The spiral flowered types are represented by such flowers as Trollius and Caltha, in which there is variation with regard to the number of parts which may be present in the various whorls. Opposed to this is

a type such as Xanthorhiza, where there are usually a definite number of parts in each whorl, and the arrangement of the parts is cyclic. An intermediate type is represented by the genus Eranthis where we get a tendency to the cyclic arrangement in the perianth segments, containing a definite number of parts but where the stamens and carpels still tend to be arranged spirally and vary in number. Corresponding to these obvious external changes, it was felt that there would be some reflection upon the internal anatomy, and that the spiral arrangement in the primitive types might, in some way, elucidate the conception of the polymorphic carpel.

Another factor in favour of the study of the Ranunculaceæ is the question of the ease with which the material could be obtained. Most of the material was obtained from the Royal Botanic Garden, Edinburgh, excepting Caltha palustris which was, of course, found in the field, and Trollius - a garden variety being used, as it was impossible to obtain the wild form. Warmest thanks are here tendered to Sir William Wright Smith for his generosity in supplying material without which this investigation would have been impossible.

METHOD

The manner in which the material was treated may be considered under three main divisions:-

A. The preservation of the material for sectioning.
   (1) The collection of the material.
   (2) The fixation.
   (3) Schedule followed for embedding.
   (4) The staining.

B. The preservation of the material to show the venation of the carpellary wall without sectioning.
   (1) Fixation.
   (2) Maceration.
   (3) Staining.

C. The fresh material impregnated to show the veining of the carpellary wall.
   (1) Dr. Gourlay's method.
   (2) Impregnation with Eosin.
   (3) Method of mounting.

A. (1). The material was collected and fixed as soon as it was brought into the laboratory. Young flower buds were fixed in the field as

soon as they were cut, thus preventing any plasmolysis. When the material was sent by post, the flowers were immediately placed in water under a bell jar and allowed to remain thus for varying lengths of time, normally five to six hours, then being fixed. In all cases the bracts, sepals, petals and stamens were carefully cut off, just above their insertion on the receptacle. This allowed the fixing agent easy access to the carpellary structures, and allowed of rapid penetration and fixation.

(2) Various fixatives were used, but it was found that, on the whole, the best results were obtained by using either Bonius fixative or Chromacetic - Chromic acid - 1 grm., Glacial Acetic acid 1 cc. and Water 100 cc. Owing to the amount of washing in 70% alcohol required after the use of Picric acid, and a consequent tendency of the material to be hard, as a general fixative chromacetic was used regularly. This gave good results with

all the species, and also at all the various stages of development. Young flower buds were fixed in 2BD, or Flemmings. This yielded good results. It also allowed of the development of the ovule to be traced, and the stage of differentiation was readily identified. Blé's was frequently used. Where the investigation merely involved the tracing out of the course of the vascular bundles, this was adequate fixation. It was too coarse a fixative, however, for the finer structure - such as that of the cells in the conducting tissue. Also in view of the fact that Gentian Violet was used as a general stain, after this fixative the staining lacked brightness.

Carnoy , 10% formalin, formalin acetic alcohol, were also used occasionally, but as in Blé's the actual structure of the carpel wall tended to be plasmolysed.

(3) The schedule used in the preparation for embedding was that of La Cours (55) but with modifications. The material was

taken from 3:1 xylol absolute, into pure xylol and allowed to remain there for four hours. Wax was poured into a dish, a well cut out the centre and replaced by xylol. Into this the material was put, the whole placed in an embedding oven. The material was allowed to remain in the oven for about forty hours - depending upon the bulk of the material. The xylol wax mixture was replaced by pure wax which was changed several times, finally just previous to the actual embedding. The wax used was a mixture of about 8 parts 52° M.P. to 1 part 45° M.P. in the winter and either 52 alone or 54 M.P. in the summer.

(4) Various stains were used but the best results were obtained from Gentian Violet as a single stain, and Safranin and Light Green for a double stain. The former was used especially when the course of the vessels was being followed in the receptacle. The staining was affected by floating the wax ribbons on a very weak aqueous solution of

Gentian Violet (aqueous), instead of in pure water as is the usual procedure. The excess stain was poured off and the ribbons allowed to dry. The wax is dissolved, as usual, in xylol. At this stage the sections were examined under the microscope. If overstained, the excess was extracted by washing rapidly in a mixture of xylol and absolute alcohol (in the proportion 3:1 or even less absolute) and immediately replacing in xylol. Clove oil did not appear to be able to remove the excess Gentian Violet, or at least it was such a slow process that it was practically impossible. This is a very quick and effective method of staining, if successfully carried out, the results were almost as good as those obtained by using Gram's Iodine method, as regards the staining of the actual cell walls, but not as regards the cell content. In order to follow the detail of the conducting tissue, sections were stained in Safranin and Light Green.

B. (1) The schedule followed was that given by Barrett (8), with various modifications. It was found better to heat the material in methylated spirits to extract the chlorophyll, then for a very short time in Eau de Javelle and left overnight in the cold good results were obtained. Staining was carried out with ammonical fuchsin. The cell walls of the outer epidermis retained the fuchsin, so that it was difficult to follow the course of the bundles. With ripe dehiscent fruits it was possible to use this method successfully, as the outer hard wall could be easily removed, following maceration.

Later it was found that equally good results were obtained if the fruits were boiled in water for some time and then transferred to warm Eau de Javelle. The hard outer wall could be removed with forceps quite readily. The flattened carpel was washed in water and mounted in Eosin Jelly or Gentian Violet Jelly and left overnight. On examination, it was found that the veins stood out clearly and

the course of individual vessels could frequently be followed.

Similarly as a macerating agent, Schultz and Chromic acid were used and yielded successful results.

C. Another method of staining the veins to show the secondary venation of the carpel wall was allowing plants to transpire in eosin for a time, If allowed to transpire for too short a time, the lateral veins were not stained, and if allowed to transpire for too long a period, the eosin penetrated into the surrounding ground tissue, masking the vessels. The carpels, as in the above group also, were split down the margins and then opened out as a flat structure. If mounted in 5% glycerine the course of the bundle could be followed easily. These mounts, of course, had to be studied and drawn immediately as they were not permanent. Some were mounted in Glycerine Jelly but it was found that the dye was taken out of the veins by the jelly. To overcome this difficulty,

the carpels were mounted in Eosin Jelly, and if ringed, these were, more or less, permanent preparations.

This method was unsuccessful in the case of Winter flowers - such as Helleborus and Eranthis. The flowers wilted previous to the penetration of the dye into the secondary lateral veins.

In the flowers and fruits which were macerated and injected with red ink each carpel was removed separately and mounted. All the carpels belonging to a single flower were labelled, so that it was possible to trace any variation which occurred within a single gynoecium.

The fruits to be macerated, or the flowers after injection with ink, were carefully split down the margins which came apart quite readily, giving a curved leaf-like structure which was difficult to flatten out in one plane and mount under a coverslip. To achieve this, the carpel was cut at the base, usually parallel to the midrib for

some distance. This was frequently sufficient to allow of the carpel being flattened. Sometimes it was found necessary to make a cut, at right angles to the marginal bundle about half way up the carpellary wall. This treatment prevented tearing of the veins, and on making drawings it was possible to restore again the exact sequence of the bundles.

In the case of the carpels injected with red ink, on mounting directly in glycerine jelly, it was found that the air present in the tissues appeared on the surface of the carpel. These were difficult to eliminate, but if the carpels were put in water or alcohol and exhausted in an air pump, then the carpels could be mounted free from air bubbles.

PROCEDURE

Each species was sectioned and investigated from the very young flower bud stage to the developing fruit, so that it was possible to record every developmental phase. For the purpose of recording the course of the vascular bundles, pp. 19-115, well developed flowers were studied. At this stage the vascular bundles are easily followed in transverse section, and these is no possibility of any post fertilisation complications.

In the Ranunculaceae, within a species, there is variation in the number of parts present in each whorl, particularly in the gynoecium, even when the other whorls tend to have a constant number of parts. Thus flowers were selected in each genus and species whenever possible, and grouped with carpel number as a basis of classification - e.g. Helleborus orientalis flowers possessing five carpels in the gynoecium were grouped separately from those possessing six carpels. The course of the vascular bundles in each group was followed separately and the results compared and contrasted. This method was adopted, as it should indicate the effect of the addition or reduction of a

carpel (or more), on the course of the vascular bundles left in the receptacle after the departure of the stamen traces within a species. It may be noted here, that it was not possible to count the variations with regard to the number of stamen traces given off in each flower, owing to the large numbers present in this family. The important fact, as regards carpellary supply, is the number of vascular bundles in the receptacle after the departure of all the traces. This number must, necessarily, be affected by the number of stamen traces to a certain extent.

If, after several flowers of each species and group (as regards carpel number) had been sectioned, and the results were found to be discordant, then many more flowers were cut until it was possible to establish a basic type, and record deviations from this in a progressive order. Although numerous flowers in each species were investigated, yet it is not claimed that these results record all the variations.

The bundles, left in the receptacle after the departure of the stamen traces, were numbered, and the course of each bundle was followed to the base of the loculus of the carpel, and then within the carpel, right up to the apex of the style.

As a result of this numbering of the bundles, and following their course in transverse serial section, it was possible to make "reconstruction" (see diagram I - XVII) in which the bundles are drawn in a longitudinal plane, and represent the receptacle, after the departure of the stamen traces, slit down one side and open out. These diagrams are drawn to scale, as an inch vertically (on paper) was made to represent a definite number of μ, longitudinally, in the receptacle. It was found impossible to record in this manner the actual size of the various bundles, and hence, in addition, to correspond to most of the reconstructions, camera lucida drawings have been made at various levels in transverse section, which illustrate the position of the bundles relative to one another as well as their actual size. To indicate the midrib bundle of the carpel in the reconstruction, a thicker line has been drawn. The actual point of departure of the midrib is not

indicated by this method, but this can be readily determined, whenever necessary, from the corresponding transverse series.

Within the carpel, the relative size of the midrib and marginal bundles are shown in the detailed drawings, taken at the same level. The behaviour of the bundles in the style is also indicated from their position and size in the detailed drawings of the stylar region. If necessary, drawings, intermediate between these two levels, were also made.

The course of the secondary vascular tissue within the carpellary wall, was recorded from the mounts of carpels, prepared by any of the methods described previously (method B and C). Camera lucida drawings were made of these preparations. If drawings were recorded from fruits, then the details of the course of the bundles in the style, had grequently to be filled in from the results obtained by the study of transverse serial sections, or younger mounted carpels, in which the style had not withered.

THE ARRANGEMENT OF THE RESULTS

The Ranunculaceae have been divided into three main groups, depending upon the arrangement of the floral organs, as follows:-

(1) Spiral flowered or Acylic Group.

All the parts are arranged spirally, so that sepals and petals do not alternate the one with the other, even though they are the same in number.

Included in this group there are the following - Trollius, Caltha, Helleborus.

(2) Semi-Verticillate or Hemicyclic Group

The sepals and petals (or perianth and honey leaves) are arranged in alternating whorls, but the remaining parts are spirally arranged. Eranthis is an example of this type of flower.

(3) Verticillate or Eucyclic

The flower is constructed all through of alternating whorls. The only genus investigated in this group was Xanthorhiza.

The order in which the results have been recorded has been based primarily upon this classification, and the arrangement within the

groups has been, roughly one of descending carpellary number, slight rearrangements being made where ever necessary, so that the whole presents a sequence. The following is a complete list of the genera and species studied in their order of description:-

1. Trollius - a Garden Variety
2. Caltha palustris
3. Helleborus orientalis
4. Helleborus foetidus
5. Helleborus viridus
6. Eranthis cilicica
7. Eranthis hyemalis
8. Cimicifuga davurica
9. Cimicifuga racemosa
10. Xanthorhiza apiifolia

In each species, the description (pp. 19 - 115) commences with a brief account of the structure of the flower, the number and arrangement of the parts. Following this is an anatomical account of the course of the bundle. First there is the arrangement of the bundles in the flower stalk, the origin of the perianth supply, the effect of the departure of these

traces on the stele, the supply to the honey leaves, stamens and finally to the carpels. Within the carpel, the course of the bundles is followed in the transverse serial sections, and the details of the second lateral vascular system from the mounted specimen of carpels.

In recording these actual results (pp. 19 - 115), there is little or no discussion, which has been deferred, until after all the species have been described. All the results have been compared and summarised in the discussion which follows (pp. 116 -) 129). In this, reference is made to the individual species.

Then follows a brief summary indicating the main results of the work, and their significance with regard to the present day views on the nature of the carpels.

TROLLIUS.

The material used in this genus was a garden variety, as it was impossible to obtain the wild form, Trollius europaeus.

Trollius belongs to the acyclic group, in which, owing to the spiral arrangement of the parts the whorls do not alternate although there may be an equal number of parts in each. There are numerous perianth leaves, these varying in number in this particular variety, from ten to sixteen. Then follow an equal or greater number of nectaries stamens, and carpels, all spirally arranged.

A transverse section of the flower stalk, slightly below the region of departure of the perianth traces, shows a ring of bundles surrounding a hollow pith. The outline of the stem is not circular, but irregular, there being ridges and furrows alternating with one another. The number of ridges varies depending upon the diameter of the stem.

Corresponding to each ridge there is a large vascular bundle, and between these, in the furrows there is present a single strand or a number of smaller bundles. Sometimes there

may be a single strand, at other times three relatively larger bundles may be present: or there may be one relatively large strand and three smaller ones. These different conditions may be seen in figs. 1A and 3A. As the point of departure of the sepal traces is reached, it is found that, in some cases, the intermediate bundles fuse with the large bundles occupying the ridges, but more frequently they persist independently for a considerable distance, although they may later take part in perianth trace formation.

Figs. 1 and 2 show the departure of the perianth traces in a flower possessing ten perianth segments. For details of the course of the bundles see Appendix I.

In this particular flower it was found, that of the ten perianth segments, the first five to be developed received more traces than the following five. In the former case, five or seven traces entered the base of each segment and as a result of the departure of these traces there were five gaps in the main stele. It was found that the outermost bundles of the supply to each segment tended to fork on their passage through the cortex, so that in some cases the

number of traces at the base of a segment was seven or nine. The following five perianth segments, however, only received three or four traces and caused three gaps to be formed in the main ring of bundles . Again it was the tendency of the marginal bundles to divide, which gave a variation in the number of strands entering the base of each segment.

The vascular supply to each perianth segment is normally derived from three of the large axial bundles in the case of the first formed segments. In the supply to one segment it was noted that only two axial bundles were involved. This condition was found to occur in a few other flowers also - but very rarely. As a result of the departure of these traces the large bundles become divided up into a number of smaller strands. The small strands which did not fuse directly with the large bundles previous to the formation of the sepal traces either:-

(1) run out along with the main axial bundles to form part of a trace to a segment,

(2) lose their identity as a result of the tangential expansion of the stele.

More fruits were examined with regard to

the manner of perianth trace formation. It was found that, whatever the number of parts in the perianth whorl, five gaps were caused in the main stele by the departure of the traces to the first half of the total number of segments, while there were only three gaps caused by the departure of the traces to the remaining segments. Again it was found that there was a tendency for the outermost bundles to fork, so that the actual number of strands entering each segment varied, five, seven, or nine in the one case, and three or four in the other. In some flowers immediately on leaving the central cylinder the bundles divided, so that seven strands passed through the whole length of the cortex. Other times division was delayed until just previous to entering the base of each segment.

The main stele is now divided up into a number of smaller segments, and from these the strands are given off to supply the honey leaves, and at a higher level the stamens, (See fig. 2C and D.). In both, a single strand leaves the main ring of bundles and forms the vascular supply of the structure concerned. The gaps caused by the departure of these traces are quickly closed by the divisions of an adjacent

strand. After the departure of the last stamen trace, the first carpel midrib is formed. Fig. 3B illustrates the case where, by the resultant growth and expansion of the axis the true spiral arrangement of the stamens and carpels is lost. On the one side there are present, in the cortex, numerous stamen traces, while at the opposite side of the receptacle several carpels are sectioned with the loculus developed and ovules present.

Diagrams I, II, and III, are reconstructions of a small sections of the receptacle above the region of the stamen traces, and they illustrate the mode of branching of the receptacular bundles, also the origin of the carpellary traces. Diagram II and diagram III are reconstructions of different portions of the receptacle of a single fruit.

An examination of these three figures shows that though there are differences in detail the main vascular supply to each carpel is similar and arises, in each case, in the same way from the receptacular bundles. One of these bundles divided and, of the two strands formed, one passes out immediately, in the majority of cases, to become the midrib of a carpel. This is the rule in the

first formed carpels. The midribs pass out quickly through the cortex and enter the carpel base. As they leave the cortex it is often only the central part of the strand which becomes the midrib, two residual strands being left in the cortex. At other times only one strand is left in the cortex. The midrib passes out without branching. The bundles which are left in the cortex pass out slowly and eventually come to lie at the base of the loculus (see fig.5). The marginal strands later, when they enter the carpellary base, fuse with these small bundles.

The bundles in the receptacle, lying between the gaps caused by the departure of the midrib traces, may fuse and anastomose in various ways, but eventually give rise to the marginal supply of the carpels. In general, only part of these strands runs out to become the supply to the margins, the remaining portion persisting in the receptacle for a considerable distance, and then forming the midrib of a carpel at a higher level. Or it may yet supply one of the margins of another carpel and, at a higher level the remaining portion passes into a carpel and becomes the midrib.

In all the carpels, with one exception, there

are two marginal bundles which are derived from separate strands of the main stele, and which are distinct throughout threir course - that is they never fuse. In the exceptional case, omly one strand enters the carpel base (see diagram III) and as it approaches the placentae, it divides into two, one strand thus being present in each margin of the carpel. The marginal bundles later give rise to the supply to the carpellary wall.

In the case of some of the last formed carpels, the portion of the bundle left after the departure of the midrib passes out in the direction of the carpel base, but later comes back into the cortex and joins the bundles which, at a higher level form the marginal supply of that carpel. When the last bundles in the receptacle commence to form the marginal strands of the last formed carpels a portion runs into the pith and ends blindly. This affords a parallel to the condition obtaining in Caltha, the whole of the vascular tissue in the receptacle is not used up in the formation of the carpellary traces.

The course of the bundles in the receptacle and the carpel was studied from macerated prepararions

of the dried fruits, and also from plants injected with red ink. The various feature established from these observations were confirmed from serial sections.

An examination of these preparations showed that there was present throughout the whole lenght of the carpel the two marginal bundles and the mid-rib. This latter, however, does not remain a single strand, but gives off two branches one on each side. In no case were the two branches given off at the same level (see fig.5 A-D). Fig. 5A illustrates the type where the one branch is given off near the base of the ca rpel, but the other strand is not given off until about two-thirds of the way up the carpel. Fig. 5C shows a case where the two strands arise closer to one another.

A remarkable feature of the supply to the carpellary wall in this variety is the fact that the lower third of the wall is completely devoid of any branches from the marginal bundles. In some, e.g. fig.5 C, it is almost half way up the carpel before there is any vascular tissue present. It should be noted that the branches from the midrib do not pass out into the wall of the carpel, but

continue parallel to the midrib, and lie within the projection of the carpel which forms the midrib tissue.

The number of branches given off by the marginal bundles varies considerably. From fog. 5A it can be seen that, in the supply to the wall thirteen branches arose from the marginal bundle , while only six are seen to pass out from this strand in fig. 5D. Many of the lateral branches pass from the marginal bundles straight out to the midrib, or to the branches of this if division has occurred. A few of the strands fail to reach the midrib or one of its branches, and end blindly in the carpellary wall. Branching of the secondary vascular system is of frequent occurrence. Several of the main bundles, however, pass directly from the marginal bundle to the midrib without branching. A few of the lateral branches divide just as they leave the marginal bundle, but division is more frequent as the strands approach that portion of the carpellary wall which lies near the midrib tissue. Anastomosis may or may not occur. (Compare figs. 5B and 5D). It is not of very frequent occurrence in any one carpel, but uusually one or two branches anastomose.

Towards the apex of the carpel, five or seven strands enter the base of the style depending upon whether the last lateral from the marginal bundle has fused with the branches of the midrib or not. At a slightly higher level there are only five bundles present. The marginal bundles pass round as the style narrows and soon fuse with the midrib branches. Thus there are now three bundles in the short style. The behaviour of these bundles is found to be variable and the following conditions are found to occur:-

(a). The midrib may die out just above this region and the combined bundles (i.e. the marginal bundle plus the branch of the midrib) continue alone to form the vascular system of the style. This is the condition most frequently found.

(b). The three bundles may continue up the style and all end blindly at the same level near the apex of the style.

(c). The midrib may continue alone to the top of the style, the marginal bundles dying out a considerably distance below this level.

Fig. 6A and 6E show the midrib in transverse section at various levels. Fig. 6A is at the base of the carpel and shows the midrib as a single

strand. It will be noted that there is present relatively more xylem than phloem. Above the phloem there are several cells with thickened walls. Fig.6E is a section about half way up the loculus and shows both the branches of the midrib have been given off. In the central portion there is very little phloem present, all having practically disappeared. The sclerenchymatous thickening is still present on some of the cell walls. In the branches, it will be noted that there is no phloem accompanying the xylem, but that the thick walled cells are present. Fig.6D shows the marginal bundle corresponding to the midrib shown in fig.6A. Fig.7A is a section above the level of the loculus, and shows the relative size of the bundles, in a type where the midrib persists for some distance up the style. There are now only three bundles, and these consist of xylem vessels, the phloem and sclerenchyma having entirely disappeared. In fig.7B, only the xylem vessels in the marginal bundles, which have fused with the branches of the midrib, remain. In a short distance there is no vascular tissue as the stigmatic surface is reached.

Thus in Trollius it is a single bundle which passes out to become the midrib of a carpel, part remaining in the cortex, which at a higher level,

after fusion with other bundles, becomes the marginal supply. Two separate strands enter the base of each carpel, these remaining distinct, so that the marginal bundles do not fuse. In an exceptional case only one strand may enter to form the marginal supply. Division occurs so that there are two bundles present at a higher level. A very important fact is that, in the majority of cases, only a portion of a receptacular strand enters the carpel, part remaining in the receptacle to form a midrib or a marginal bundle of a carpel developed at a higher level. Again the bundles divide so that part only passes out, and so on till only a few carpels are to be supplied. In the last formed carpels the whole supply may pass in without division. All, however, may not be used in the formation of the carpellary traces, part remaining receptacular and ending blindly in the pith at a higher level. In the carpel the midrib gives off two branches, which continue to run parallel to it. The branches from the marginal bundles fuse with the midrib or its branches, a few ending blindly in the carpellary wall. It will be noted that there is variation in the stylar supply.

CALTHA PALUSTRIS.

The flower of Caltha consists of from five to seven large yellow perianth segments, followed by many spirally arranged stamens, the number of which varies from eighty to a hundred and fifty. This spiral sequence is continued in the gynoecium, this consisting of carpels varying in number from five to fifteen.

The pedicel is ridged and furrowed, the ridges varying in size and depth. The vascular tissue consists of a ring of bundles surrounding a hollow pith. Corresponding to each ridge there is a large vascular bundle, but two may be present if the ridge is large. In the furrows one, sometimes two smaller bundles occur. The number of ridges varies from flower to flower, and therefore so does also the number of large vascular bundles present. A ridge bundle may give off a trace, which passes out through the cortex and comes to lie centrally at the apex of the ridge. Surrounding each bundle there was in some flowers a continuous band of sclerenchyma two to three cells deep, this apparently being associated with the types found in the drier situations.

As the flower stalk broadens out into the receptacle, branches become detached from the larger bundles and occupy a position within the vascular ring, near the parent bundle. Later the large bundles divide to give rise to the traces of the perianth segments. As the point of departure of these traces is reached, it is found that the large bundles expand tangentially, vessels running out towards the right and left round the receptacle and fusing with the adjacent receptacular bundles. In the majority of cases, there is a central portion which, at a higher level, becomes the midrib of the corresponding perianth segment. (See fig. 8A) This central portion or part of it may, however, remain receptacular. (See fig. 8C and D). It may form the whole supply to one perianth segment as is shown in fig. 8E. The vascular tissue which arose as the result of the tangential expansion of the ridge bundles fuses with the bundles in the furrows. It is from this complex that the marginal traces, and in some instances also, the midrib traces arise. As the traces pass out to each segment, there is at the same time a separation of the individual bundles which run longitudinally.

Normally three traces leave the central

cylinder and pass out through the cortex to each segment, but occasionally four are formed. One, two, or three gaps may be formed in the vascular ring of the receptacle as the result of the departure of these traces. There is some variation as regards the position of these relative to one another, and to the intermediate bundles formed after the tangential expansion of the ridge bundles. Fig. 8A to F illustrates this variation which occurs when the three bundles leave the main stele to supply each segment. In fig. 8A and B three separate gaps are caused by the departure of these traces, and shows the position of the gaps relative to one another. In fig. 8C and D only part of the central portion passes out, traces arising from its flanks. Fig. 8F illustrates a type where only two gaps are present due to the outward passage of two adjacent bundles. As in the case of the three gaps, one or two bundles may be present between the gaps. Only the central portion of the expanded ridge bundle forms the whole supply to the corresponding perianth segment in fig. 8E. On its outward passage through the cortex this trace divided into three.

From these figures it will be seen that

branching of the traces may or may not occur. Branching of the midrib is almost as frequent as that of the marginal bundles, in both cases, occurring in the cortex previous to entering the base of the segment.

As the result of the formation of the perianth traces, the stele has become divided into munerous small bundles. It is from these that the supply to the stamens is given off. A receptacular strand may give off a trace or it may divide into three, the central portion forming the supply to one stamen. Fusions occur between the receptacular bundles in the latter case, so that there is a tendency to keep the number of bundles more or less constant.

The carpellary traces are formed at a higher level. The bundles supplying the midrib of a carpel persists for some time as an individual strand opposite the apparant base of insertion of the carpel. Just as in the perianth supply, here again, there is variation in the origin and method of departure of the traces. Using this variation as a basis, it is possible to divide the flowers examined anatomically into four main groups.

The first type is represented in figs. 9 and 10, and in the reconstruction, diagram IV. The outward passage of the midrib involves only the central portion of the bundle, there being two small bundles left in the receptacle, one on either side of the gap. These strands with or without fusion with another receptacular bundle form a portion of the marginal supply of that carpel. These two small strands may enter the carpellary base without fusion with any receptacular bundles, but a single bundle enters at a higher level. This fuses with one of the small strands, and thus there is present, in a marginal position at the base of the carpel, one large and one small bundle. To counteract this inequality division of the larger bundle occurs and the final result is the presence of two marginal bundles of equal size. One of the small strands may fuse with a receptacular bundle, so that a large and small bundle enter the base of the carpel, division taking place within the base as previously.

Fig. 9A shows the appearance of the receptacle after the departure of the midrib traces. The two bundles on either side of the gap can be seen in the receptacle opposite the base of each carpel. There are present four larger bundles, each of which, at

a higher level, divides into two, the portions becoming the marginal bundles of two carpels. In Fig. 10, the bundles at the base of each carpel are dividing, so that two equal portions result.

It will be seen from a consideration of this figure that the pith is traversed by numerous bands of phloem. These arise during the bundle fusions and divisions which characterise this level of the receptacle. At first, they are accompanied by a few xylem vessels, but these end blindly on entering the pith. At this level the pith is now a solid structure. Gradually this parenchyma fails to be developed, and the carpels become free the infolded margins appearing at a higher level.

Another flower presented somewhat similar characteristics in transverse section, but here, the two bundles left after the departure of the mid-rib from the single strand, in all cases but one, immediately pass out into the carpellary base. (Compare figs. 9A and 11B.). These two strands are also reduced in size. Again the intermediate bundles may divide to supply two carpels, or the whole passes into one. When two bundles enter the base they fuse with the two small bundles already present to form the marginal supply.

From fig,11A and B, bundle 20, and diagram V, it will be seen that a strand passes in towards the pith, divides into two and fuses with part of the marginal supply of two carpels, but not neighbouring ones as they have become free from the receptacle. In one carpel where two strands enter, besides the two small bundles, they fuse to form a single concentric strand within the carpellary base, but divide at a higher level to give the two marginal bundles.

In another flower similar to the above, in the supply to one carpel a single receptacular strand divides into three equal parts, the central portion forming the midrib, the two remaining portions, equal in size to that given off, form the marginal supply at a higher level. A very small receptacular strand fuses with the one bundle, previous to its entering the carpellary base. (See fig.11C, bundle X). Thus, in this case a single strand has formed, practically the whole supply to one carpel.

The third type presents striking differences from the other two main types. It will be seen from the reconstruction (diagram VI) that in many cases a single strand divides into two, part

passing out to form the midrib, whilst the otherpart equal in size to that given off, remains within the central cylinder (see fig.12A, B, and C.). On the outward passage of the midrib the small strands characteristic of the second type were again given off, but this time in the cortex, or within the carpellary base itself. (See fig.12C). In the case of one strand, bundle 12, the central part passes out as the midrib, one part remains as a receptacular bundle for some distance, while the other part runs out immediately through the cortex and comes to lie at the base of the loculus. Bundle 11 divides into three equal parts, the central portion becoming the midrib of a carpel, the remaining two parts fusing immediately with the other adjacent receptacular bundles. In every case two separate strands enter the base of the carpel to form the marginal supply, and remain thus without fusing. It will be seen from the reconstruction that a receptacular bundle divides and supplies one placenta of two carpels. In the other cases there are present between the midrib gaps two bundles, each of which supplies a single placenta, Where a single bundle supplies two placentas, it would appear to be due to the fusion of the bundles in the receptacle. It will be seen that a strand passes

from bundle 14 to bundle 12 - similar to one of the bundles in the second type.

The fourth type more closely resembles the thrid than any other type yet described, but presents striking differences from this. Fig. 13A, B, and C, represent the bundles in transverse section at successively higher levels, while diagram VII is a reconstruction of the bundles above the level of departure of the stamen traces. It will be seen that the whole of a receptacular bundle passes out to become the midrib of a carpel in two instances, namely bundles 5 and 9. The one bundle as it passes out through the cortex gives off two small traces, which come to occupy a marginal position. The other bundle only gives off a single trace. In the midrib supply to the other carpels a large receptacular bundle gives off a trace. The portion of the bundle remaining in the main ring o f vascular tissue, divides at a higher level, and these two traces pass out immediately, one to each adjacent carpel, to form the supply to one margin. Thus, in this particular flower a single bundle may supply the midrib and give off a small trace on its way through the cortex, or a single bundle may supply the midrib, and this again gives off traces on its passage

through the cortex, and the one placenta of that carpel, also the adjacent placenta of a neighbouring carpel.

We may summarise the various types in the following manner:-

(1). A single bundlessupplies the midrib and both placenta of that carpel.

(2). A single bundle supplies the midrib and the one placenta of that carpel, also the adjacent placenta of a neighbouring placenta.

(3). A single bundle supplies the midrib and two separate bundles form the marginal supply.

(4). A single bundle supplies the midrib, and leaves in the receptacle two smaller bundles which later form part of the marginal supply.

(5). A single bundle passes out to supply the midrib, and on its way through the cortex leaves two small strands, which enter the carpellary base. At a higher level one or two strands may enter and fuse with these.

Thus we have a complete sequence from the type where a single bundle supplies the midriv and two placenta, to the type where three separate strands supply each.

At the base of each carpel there may be present two or three bundles - the midrib and one or two marginal bundles. In the majority of the flowers sectioned there were present two bundles of equal size, but at a higher level they may fuse. In other cases two bundles of unequal size were to be found, and these normally fused for a short distance, dividing later into two equal strands. Separation of the bundles occurs previous to the insertion of the first ovule.

From the serial sections, it was seen that branching of the marginal bundles was frequent above the insertion of the first ovule. These secondary bundles supplying the ovary wall did not pass as far round as the midrib tissue. One or two branches appeared to arise from the midrib bundle itself near the base of the carpel.

Fig.15A to G illustrates the details of the secondary supply to the carpellary wall, and shows the variation which occurs in this venation. This variation is not only found to exist in different plants, but also in different carpels of the same flower. For example, fig.15E and D are carpels from one flower.

Examination of these figures reveals the fact that towards the base of the carpel, the ovary wall may be supplies by vranches from the midrib, as well as from the bundles in the margins, while in the upper half the margins alone give off the whole of the secondary venation system. These particular figures have been selected especially to show the types of branching of the traces from the midrib bundle. In many fruits the midrib is unbranched, as for example in fig.15D. Thomas ( ) in his description of Caltha states that the midrib is entirely unbranched. The branches of the midrib may be poorly developed (see fig.15C and G) only a single small strand being given off, which is not branched and does not anastomose with the branches from the marginal bundles. In fig.15B there is only a single trace given off from the midrib, but here it is branches and anastomosis with another secondary carpellary bundle. Fig.15F illustrates a case where the carpel wall near the base is supplied by a branch from the midrib bundle. This is a large much branched vein. In this particular area of the wall there are no branches from the marginal bundle. In fig.15E and G there are three separate traces from the midrib, which are more strongly developed in the one carpel than in the

other. One trace runs from the midrib to the marginal bundle unbranched, the other two passing out unbranched for varying distances into the carpellary wall. (See fig.15E).

The secondary vascular supply derived from the marginal bundles forms the main supply in the carpellary wall. Branching may occur just as the traces leave the main bundles, but more commonly well out in the carpellary wall itself. These traces do not approach the midrib tissue, all ending blindly in the wall at varying distances from the midrib bundle. These secondary bundles may or may not anastomose (see fig.15B and D). The carpels in which anastomosis occur present more complicated systems of venation than the others. The veins in the upper half of the carpel tend to be more strongly lignified than those developed at a lower level.

The style in Caltha is very short and terminates in a well developed stigmatic surface coverdd with large papillate cells. As in the other parts of the carpel, so in the style, there is variation as regards the vascular supply. The following types have been found:-

(1). All three main veins pass into the style, remain unbranched and do not fuse with one another, (See fig.15E).

(2). All three may pass up into the style, but each branches several times, so that a semicircle of vessels surrounds the stylar canal. (See fig.15A.).

(3). The midrib may continue up the style, the marginals ending blindly at the base. See fig.15D.

(4). The midrib may divide into two at the base of the style and each part continue up the style, as is shown in fig.15D. In this case also, each of the marginal bundles branch once and continue parallel to the midrib for varying distances up the style.

Fig.16A shows in longitudinal section a carpel, in which numerous branches are being given off by the midrib, and fig.16B shows the origin of one of these branches in detail. In fig.17A the midrib and marginal bundles have fused in the style to form an arc of vascular tissue surrounding the stylar canal. In fig.17C the marginal bundles in the style have become reduced , there being no phloem present and only two xylem vessels. The midrib has divided, a portion being detached on either side - as is shown in Fig.17C and in detail in fig,17B.

Thus in the flower of Caltha there is variation with regard to:-

(1). The number of component parts in each whorl.

(2). The origin and mode of branching of the traces to the perianth segments and the carpels.

(a). In the perianth segments one, two, three or very seldom four gaps are caused by the departure of the traces to each segment. In the case of a single gap the trace immediately divides into three. In all the other types branching may or may not occur in the cortex, in the midrib as well as in the marginal bundles. Thus there is variation as regards the number of traces entering each segment.

(b). Supply to the carpel.

All types are found from a single bundle supplying the midrib and both margins of a carpel, to separate bundles supplying all three. Normally three traces enter the base of each carpel, sometimes five, when the branches of the midrib strand enter previous to the main marginal supply.

(c). The supply to the carpellary wall.
The marginal bundles may give rise to the whole of the secondary vascular supply. The midrib, however, may give rise to traces which vary in size, in number, and in degree of branching. Anastomosis may or may not occur between the secondary lateral branches,

(d). The supply to the style.
All possible variations are found to occur here.

HELLEBORUS.

In this genus three species were studied,

(1). Helleborus orientalis.

(2). Helleborus foetidus.

(3). Helleborus viridis.

Helleborus orientalis.

The flower in this species has usually five, sometimes four, greenish white perianth segments, twelve to thirteen nectaries, a large number of stamens, and five to six carpels. In every case a bract subtends the flower.

A transverse section of the flower stalk below the region of departure of the perianth traces, reveals the presence of ten bundles surrounding a large parenchymatous pith (see fig. 18A.). The cortex is about ten to twenty cells deep. Above the region of departure of the traces to the bract, there are usually divisions of the five bundles present, so that ten distinct bundles are present at a higher level. Of these two different types may be distinguished - (1) those which are radially elongated, (2) those which are tangentially elongated. The former at a higher level will form the vascular supply to the perianth segments, while the latter supply the remaining whorls.

A radially elongated bundle usually divides into three equal parts, whilst still lying within the central stele. (See fig.18B). Sometimes, however, a trace is given off, and later on the opposite side another trace, while the remaining portion passes out at a higher level. (See figs.18D and 19B and C). Of these strands, the central portion forms the midrib, which remains entirely unbranched as it passes out through the cortex. The two marginal bundles each divide into two, usually just previous to entering the base of the perianth segment, so that the vascualr supply consists of seven bundles. In fig.19C three of the marginal perianth traces have been given off branches. In the one case seven are entering the base of the perianth segment, in the other five are seen passing out through the cortex, while in the third, one of the marginals is just giving off a trace. Thus all five of the radially elongated bundles pass out to form the perianth supply, one primary axis bundle to each segment.

Meanwhile the other five main vascular bundles of the flower stalk have commenced to divide. In all the cases the bundles become even more tangentially elongated. (See fig. 18C). The two ends curve outwards, so that the bundle has now become

concave to the outer epidermis. The curvature becomes progressively more marked until eventually a complete cylinder of xylem elements has been formed, enclosing within some phloem and cambial cells. The pseudo-concentric bundles thus formed give off branches, which may, in turn, divide so that a system of cortical bundles, also pseude-concentric in character, results. The details of this process are shown for one peduncle in figs. 18A to D, 19A to D, and 20A to D, and the detail of one bundle in fig. 21A to D. Following this development of the cortical bundle complex, a secondary simplification results largely owing to the reunion of these bundles with the parent bundle. Some of the smaller cortical bundles pass out as the vascular supply to the lower nectaries, each nectary receiving a single trace. As a result of the behaviour of the bundles, there are present two bundles in place of the original tangentially elongated bundle, and, out in the cortex, a trace, which will supply the first formed nectaries.

The bundles in the main ring now expand in a tangential direction, and each gives rise to three bundles, the central one passing out to supply a nectary developed at a higher level. The gaps caused by the departure of the perianth traces are

now closed, and the receptacle contains a ring of vascular tissue consisting of numerous small bundles. These divide and give off traces to the staminal whorl, each receiving a single trace.

After a number of stamen traces have been given off, the receptacle narrows, and there is a reduction in the number of bundles present due to fusion. Again, as in Caltha, owing to the spiral arrangement of the floral elements towards the apex of the receptacle, stamen traces can be seen passing out through the cortex, while at another point the carpellary midrib is commencing to pass out. The gaps of the last five of six stamen traces fail to close previous to the outward passage of the midribs, and normally remain thus. Five or six midribs may be seen passing out through the cortex, or lying in the carpellary base, as is shown in fig. 22F. The remainder of the vascular tissue in the repectacle becomes grouped into a series of paired bundles - two opposite the base of each carpel. These bundles pass into their respective carpels, and form the marginal supply. No trace of any vascular tissue is left in the receptacle, nor do any vessels pass into the pith. The whole is used up in the formation of the carpellary traces.

In all cases the midrib passes out rapidly through the cortex without branching, and comes to lie within the base of the carpel. In its rapid passage through the cortex, the midrib contrasts markedly with the marginal bundles which pass out much more slowly.

It will be seen from a study of diagram VIII, which is a reconstruction of the vascular supply to the carpels of a flower, and fig. 22 with the corresponding bundles in transverse section, that the origin of the midrib to the carpels varies. Five carpels are present in this particular series, and in four of these, a single strand gives rise to the midrib of a carpel, also the supply to one margin of the carpel without or with our fusion with another receptacular bundle. In the other case a single bundle gives rise, not only, to the midrib, but also to the supply to both margins of that carpel, without fusion with other bundles. The vascular supply to adjacent placenta of neighbouring carpels is not fused. In the case of strand number 4, a small bundle passes from this to bundle number 5, but this is previous to the bundles becoming carpellary traces. Bundle ten divides one part passing to fuse with bundle 9, the other forming the supply to one margin of a carpel.

After the departure of the midrib traces, from the bundles on either side of the midrib gap a strand passes out through the cortex and comes to lie along side of the midrib, but never fuses with it. (See fig. 22F and fig. 23A). These strands do not arise simultaneously, one always passing out at a higher level than the other. This occurs in the case of four out of the five carpels. The exception will be dealt with later. These strands arise at various levels after the departure of the midrib, but in all cases are derived from the actual marginal carpellary bundles, and never from the receptacular ones. It should be noted, however, that the bundles still lie well outside the carpellary base, when these primary traces are given off. They may sometimes be given off when the midrib is still within the cortex. Thus we have the midrib, and just below it on either side, the two accessory strands which accompany it, all three of which enter the carpel base together. They pass straight out through the centre of the base of the carpel. These branches may not be given off until after the midrib has entered the carpel base, in which case, after entering the base they curve round the carpellary wall, just as if the loculus had been developed.

These primary traces although they are normally unbranched, may, in some instances, branch either at the base of the carpel, or near the midrib. In both cases only one strand comes to lie parallel to the midrib.

After the departure of these primary traces the marginal strands approach one another. Fusions occur between these strands supplying each carpel, but there is variation in the level at which this takes place. The fusion is very complete, the xylem elements of the bundles becoming completely intermingled, so that the strands lose their individuality. This single strand is concentric with the xylem centrally placed. This fusion may occur just after the departure of the primary traces - that is as the bundles pass out through the cortex. In this case a single strand enters the base of the carpel as the marginal supply. The bundles may not fuse, however, until after they have entered the carpel base. Here, as in the previous case, the fusion of the bundles was very complete, with a single bundle occupying a central position in the base of the carpel. In an intermediate type, the vessels in the two strands just approach one another as they enter the carpel base, the fusion not being complete until the

bundle is within the carpellary base. In this case, and in the one mentioned first, there is a two trace system at the base of the carpel, instead of the typical three trace system. This reduction in number is obviously due to fusion.

This fusion bundle persists for a considerable distance. Branches may or may not be given off from this to supply the ovary wall. As the point of departure of the first funicular trace is reached, the bundle divides into two, the strands passing to right and left respectively to occupy the normal position of the marginal bundles. In no case did the funicular trace arise from the fused bundle.

Before this level, the carpels have become free from one another, owing to the disappearance of the connecting parenchyma. The margins of the carpels have also become delimited. As the two bundles separate the infolded margins make their appearance. This infolding marks the point of attachment of the first ovule. Here the epidermal cells are enlarged, and the opposing margins press closely against one another.

It was noted that in one carpel of this flower, the primary traces were not given off by

the marginal bundles. This carpel is definetly abnarmal, as was confirmed after several other carpels were sectioned. Almost as soon as the midrib passes out from the central cylinder, the bundles on either side of the midrib gap fused before any traces were given off. At a higher level, it was found that this carpel was open for some distance, the ovules being developed, not in the normal region of the placenta, but on that part of the carpel margin, which would normally have been in contact with the opposite margin.

To find out if this variation in the vascular supply to the carpels of a flower were of general occurrence or not, many more fully developed flowers were sectioned.

Diagram IX shows the vascular supply to a flower with five carpels in the region of the carpellary base. Here again the last five or six stamen gaps fail to close, so that the receptacle at this level, presents an appearance similar to that already described. In every case a single bundle gives rise to the midrib and part, if not all of the vascular supply to one placenta of that carpel. To all the carpels, we again get the two primary traces passing out, and occupying a position near

near the midrib. These may be given off soon after the departure of the midrib or at a much higher level. Two marginal strands always enter the carpel base separately, and fuse at a higher level within the base of the carpel. Here also, branches may or may not arise from the fused bundles. Thus in this flower the course of the bundles is very similar to that described above with minor differences.

Diagrams X and XI are reconstructions of the vascular supply to the carpel base in two flowers each possessing six carpels.

From diagram X, it can be seen that, in the case of three carpels, a single strand gives rise to the midrib and part, if not the whole of the marginal supply to one placenta. In the other three carpels, a single strand divides into three, the central part of which passes out to become the midrib while the two remaining parts form the supply to the two margins, with or without fusion with adjacent receptacular strands. Although there are a greater number of carpels in this flower, yet we do not have an increase in the number of bundles in the receptacle after the departure of the stamen traces. The receptacular bundles divide and give off traces

to adjacent bundles, so that the receptacle presents a much more complicated appearance than in the previous case. It will be noted that the bundles supplying adjacent margins of neighbouring carpels are fused in two of the carpels. (See diagram X, bundles 8 and 9). Again the primary traces are given off , two to each carpel, and the marginal supply enters the base of the carpel as a single strand in two carpels.

Diagram XI shows that one bundle divides into three the central part passing out to form the mid-rib, and the remaining two parts form the marginal supply, in the one case after fusion with other two receptacular bundles. The marginal supply to two carpels is fused for a short distance. Here, however the receptacular strands do not give off strands to adjacent bundles, and hence the reconstruction appears much simpler than that shown in diagram X. The primary traces may be seen here also, and the marginal bundles do not fuse until they have entered the carpellary base.

We may, therefore, summarise the conditions obtaining in Helleborus orientalis by stating that receptacular bundles may:-

(1). divide to give rise to the midrib, and the

whole supply to that carpel, with or without fusion with other receptacular bundles.

(2). give rise tp the midrib and the supply to one margin of that carpel, again with or without fusion with other receptacular bundles.

The midrib is always entirely unbranched. Just as the marginal bundles start to become orientated, a well developed strand passes from each and comes to lie along side of the midrib. These bundles do not arise simultaneously. They may be given off while the midrib is still within the cortex, or after it has entered the carpel base. In the first case, the strand usually passes straight out through the centre of the carpel base, whilst in the latter, it may follow this course, but normally curves out round the carpellayy wall. This trace is usually unbranched, but forking may occur at the base or near the midrib, or at both points. One of these branches runs parallel to the midrib, the other fading in the wall. The marginal bundles may fuse in the cortex, just as they enter the carpel base, or with in the base of the carpel. In all cases division of this bundle occurs about the level fo insertion of the first ovule, and at this level the margins become

delimited. Branches may or may not arise from the fused marginal bundles.

From examination of the serial sections it was seen that strands passed out from the marginal bundles, curved round the carpellary wall, and eventually ran parallel to the midrib, but never fused with it. Fig.23D shows the position of these bundles at the base of the carpels. The details of the secondary vascular supply in the carpellary wall were studied in the mounted specimens of whole or half carpels.

Above the level of the last ovule, it was seen that the amount of xylem in the vascular bundles of the placentae had diminished. Compare Figs,24B and D. In some flowers there was no lignified tissue whatsoever. The vessels are still present in the accompanying strands on either side of the midrib - which were derived from the marginal bundles. Just at the base of the stylar canal the lignified vessels again appear in the marginal strands, and are developed to a greater extent than previously. Similarly there is an increase in the number of vessels present in the midrib bundle. Fig.24A and B are drawings of the midrib and marginal bundle at the base of a

carpel, shown under low power in fig.24C. Fig.24D shows the appearance of the marginal bundle above the last ovule, while fig.25A is a drawing of the bundles at the base of the style. It will be seen that the traces are still present on either side of the midrib. The marginal bundles, now strongly developed, slowly pass round towards the midrib, and come to lie naer the bundles flanking the midrib. Thus at the base of the style there are present five bundles. This condition persists for a considerable distance. Fusions occur between the marginal bundles and their lateral branches. These become divided up in various ways so that there is a mass of xylem vessels forming a horse shoe or a circle of vessels below the midrib, and surrounding the apex of the stylar canal. This condition persists for the greater part of the long style. Although there are groups of vessels detached from this combined bundle, consisting of the marginal bundles and their lateral branches, the groups do not fuse with the midrib. It should be noted that there is no phloem associated with the marginal bundles at this level, and very little with the midrib. A short distance from the apex of the style, the marginal bundles fuse with the midrib, and form a single strand which ends previous

to the stigmatic surface being reached. This bundle is seen in fig. 25C.

Fig. 26A to C represents the vascular supply to the carpellary wall up to the point where the bundles enter the base of the style. It will be noted that the bundles present in the ovary wall all arise from the marginal bundles, while the midrib remains unbranched. It will be seen from an examination of these figures that these lateral strands leave the main bundles and may branch at any point on their course round the ovary wall. It is very frequent near the midrib, but occurs also just as the strands leave the marginal bundles, and at any intermediate point. In some cases the secondary strands do not divide, especially those towards the base of the carpel. The behaviour of these strands as they approach the midrib is characteristic of this species. The strands, which pass round as far as the projection which forms the midrib tissue, so not fuse with the midrib bundle, but curve sharply at right angles to their course, so that they come to lie parallel to the midrib, and continue thus for some distance, and then end abruptly. Meanwhile, a strand developed at a higher level of the carpel comes to occupy this position

near the midrib. In some cases this strand fuses with one which has persisted from a lower level, and both continue parallel to the midrib for a short distance. Then they die out and are replaced by another strand at a higher level. As a result of this, there is always a strand present on either side of the midirb, but this is not a single strand which has persisted from the base to the apex of a carpel. As we approach the apex of the loculus it will be seen that a strand persists on either side of the midrib, and enters the base of the style. This lateral bundle is not necessarily derived from the last branch of the marginal bundle, but is frequently derived from a lateral at a lower level. (See fig. 26C). The last two or three bundles derived from the marginal bundles frequently do not pass round as far as the midrib tissue. The course of the bundles was followed from the serial sections nad has been already described.

HELLEBORUS FOETIDUS

This species differs from H. orientalis, in the colour of the perianth segments, in shape, and with regard to the number of carpels formed. Three carpels are usually developed but two occur frequently. It was found that out of the three generally present in a flower, there was very commonly a difference in size, one being considerably smaller than the other two. This difference was particularly noticeable in the ripened follicles, where it was found that sometimes only one carpel enlarged after fertilisation, the other two remaining more or less abortive. In some fruits all three were equally developed.

The flower stalk and carpels are covered with large glandular hairs. (see fig. 31, D, E & F.) These are developed at a very young stage and only die when the fruit is developing. Between the carpels and the stamens the epidermal cells of the receptacle develop into large sessile glands. Above and below this region, however, the large stalked cells with swollen heads are found. These are found on all external parts of the carpel appearing on the projection of the midrib, and at

the infolded margins. They are developed for a considerable distance up the style but are not abundant in its upper half.

A transverse section of the flower stalk just below the region of departure of the perianth traces reveals the presence of ten vascular bundles arranged in a ring, surrounding a large parenchymatous pith. As in H. orientalis there are two types of bundles, namely the radially and the tangentially elongated types. The latter pass out to form the supply to the perianth, one to each segment, after division into three. The division takes place prior to their departure from the main ring of bundles. Just before entering the base of the segment the marginal bundles divide once so that five strands enter. The midrib is unbranched (see fig. 28. B & C).

The tangentially elongated bundles have meantime become divided up into several smaller strands (see figs. 28 A & B.). Here, as in H. orientalis, the bundles expand tangentially but in this species become divided up into two, three, or four portions. These parts of the main bundle each form a concentric bundle with xylem

surrounding the phloem. Thus in this species the concentric bundles lie within the main ring of vascular bundles, instead of dividing in a radial direction as was the case in H. orientalis. In H. foetidus although some of the vessels continue to pass outwards they do not give rise to cortical concentric bundles. The concentric bundles only remain as such for a short distance. The vessels pass back towards the main strands and the concentric structure is broken down (see fig. 28 C.). The vessels run out tangentially and each concentric bundle eventually gives rise to several small strands. By this tangential expansion the gaps of the perianth traces become closed. In this species no bundles remain out in the cortex to supply the honey leaves.

By further division of the receptacular bundles the traces are formed which pass out to supply the honey leaves. Later traces pass out to supply the stamens, a single strand entering the base of each filament. These traces arise in the same way as in the other species. The receptacle becomes narrower, and there is a reduction in the number of bundles present as the bases of the carpels are reached. All the flowers studied showed the

same vascular features up to this level. At a higher level, however, strikingly different arrangements in the bundles were found to occur in the various flowers studied, and also remarkable differences in the pith were noted.

The first flower to be studied possessed only two carpels. In this, as the last stamen traces were passing out through the cortex, the strands, which at a higher level, will become traces to the midrib of each carpel, can be seen still within the central ring of bundles. (see fig. 29. A, M.). In the one case, a single receptacular bundle has divided into two, one strand of which at a higher level became the midrib of a carpel. The other main bundle divided into three, the central portion passing out as the carpel midrib. The gaps caused by the departure of the stamen traces are quickly closed, except the last two. As the midrib traces are passing out through the cortex these gaps become closed. Thus a transverse section of the receptacle at this level shows a complete ring of bundles with gaps at two points - namely the midrib gaps; the bundles on either side of the midrib gaps have expanded tangentially so that the bundles

which will become the marginal supply to adjacent margins of neighbouring carpels ~~is~~ are fused. The receptacle at this level is strikingly different from the corresponding level in H. orientalis. There the bundles did not expand tangentially to close the stamen gaps.

It will be seen from fig. 29 A to D that, in the bundles on either side of the midrib gaps, the xylem is not concentrated at one point only, but that there are four main groups and a few strands containing two or three vessels lie between these bundles and the midrib gaps. These small strands are the first ones to pass into the carpel. At about the same level, the main bundles divide, so that two bundles approach each carpellary base, one on either side of the midrib gap (see fig. 29 E.) The behaviour of the small groups of vessels is variable. In this flower it was found that they may:-

(1) pass out and fuse directly with the midrib (see fig. 29E).

(2) pass round the carpellary wall for some distance and then end abruptly.

(3) pass right round the carpellary wall and then fuse with the midrib.

Any remaining small groups of vessels enter the carpel base. Meantime, the main bundles which will form the marginal supply to the carpels, are passing out through the cortex. Two strands enter the base of each and fuse with the group of small vessels if any are present. The two bundles at the base of each carpel never fuse although they may approach one another very closely. Strands pass out to supply the carpellary wall below the level of insertion of the first ovule. At a higher level the connecting parenchyma is not present, and the carpels have become free. Above this level the margins of the carpels become delimited.

The pith in this flower is very different from that of H. orientalis. Here, in the region of the last few stamen traces the cells in the pith commence to divide actively. Nearly all the cells possess nuclei, which divide and become separated by a cell wall, which is much thinner than that of the parent cell.

The next flower to be studied possessed three carpels (fig. 30, A.). In this a receptacular bundle divided tangentially into two, one part passing

out at a higher level to become the midrib of a carpel opposite. To supply the second carpel developed a single strand divides into three, the central portion passing out at a higher level to become the midrib of a carpel. The midrib of the third carpel is derived from a receptacular bundle which has divided into two.

Again, as in the other flower examined, the gaps of the stamen traces close rapidly by division and tangential expansion of the bundles. The last three gaps are only slowly closed by the expansion of the bundles. The receptacle at this level presents a similar appearance to that previously described. (Compare figs. 29 and 30 A.) The small groups of vessels are found to behave in a similar manner. In two carpels the whole group entered the base and came to occupy a marginal position. The receptacular bundles became divided up into six groups, two bundles entering the base of each. These fuse with the small groups of vessels.

The pith in this particular flower showed the same cell division as in the other flower examined. Here however, there was a difference in that at two

points the division seemed to be focussed particularly on a few cells, so that as a result there was present a "nest" of meristamic cells (see fig. 31 C.). Again it may be noted that this condition arose just as the last few stamen traces are departing, "nests" of meristematic cells originating near the centre of the receptacle, but passing out and eventually coming to lie just beneath the xylem in the two vascular bundles. At a slightly higher level they pass out and close the stamen gaps. The tissue formed from these meristematic cells appears to be exactly similar histologically to the phloem, but are situated internal to the phloem. Later when this tissue is present between the bundles it is continuous with the phloem of the two bundles.

In another flower which was sectioned, these groups of "nests" of meristematic cells were developed to a greater extent than in the other types. These again lie internal to the phloem and later come to lie between the bundles. Thus the receptacle presents a different appearance to any yet described as all the gaps are bridged by tissue derived from meristematic cells. Similarly, after the departure of the midribs, cells pass in but do not completely

close the gaps. This tissue passes into the base of the carpel and round the wall as the first trace. The receptacular bundles separate into six main groups, and more meristematic cells close the gaps for a short distance. After the marginal bundles have entered the base of each carpel another group of cells appears in the centre of the pith. This remains in the position and dies out at a higher level. In another flower similar to that described above, the connecting parenchyma persisted after the delimitation of the margins. (See fig. 30 B.).

Several other flowers were sectioned to determine if this division in the cells of the pith, and the appearance of "nests" of meristematic cells were of constant occurrence or not. The division of isolated cells was found to be fairly frequent, being accompanied in a few cases by the meristematic groups of cells. In other cases there was no active division whatsoever in the pith. On account of this the sections presented dissimilarities in the various cases at corresponding levels.

Fig. 30 C. is a transverse section near the base of the carpels in a flower in which there are no divisions in the pith. The form of the bundles is

different from the others described. Here they are not tangentially elongated, and the bundles do not give rise to small groups of vessels. The gaps of the last three stamen traces fail to close.
There are present in the receptacle five bundles three of which are larger than the other two. Each of the large bundles divides into three, the central portion passing out as a carpel midrib. In fig. 30 C two of the midribs are just leaving the main ring of vascular tissue. One of the remaining bundles has fused with another receptacular strand whilst at another point two bundles are approaching one another and fuse at a higher level. The largest of the bundles divides into three, the central portion passing out as the midrib, while the two remaining portions form the marginal supply at a higher level, without fusion with other receptacular strands. Thus, in this case, no small groups of vessels pass in previous to the main supply and form the first trace to the carpellary wall. The arrangement of the bundles in the receptacle, and the shape, closely resemble H. orientalis, but differ as regards the number present, the lack of primary traces, and the independence of the marginal bundles. This flower

differs from the other H. foetidus already described, in the shape of the bundles, the lack of the meristematic "nests" or cell division in the pith, and the small groups of vessels or tissue derived from these "nests" which enters the base previous to the inward passage of the main marginal supply.

Another flower presented similar features in transverse section, again the lack of cell division being a marked feature. In this case, however, the strands which form the adjacent marginal supply to two neighbouring carpels are fused in the receptacle (see fig. 30 D.). This single strand divides into two parts, one of which passes out to supply the adjacent margins of two carpels. Here also the origin of the midrib is variable, a single receptacular strand dividing into two one part immediately becoming the midrib. To supply another carpel, a single bundle divides equally into three, whilst in the third carpel again there is division into three but the two remaining strands are of unequal size.

This flower resembles H. orientalis even more closely than the previous example. Here there is the variation in the origin of the midrib, and the fusion of strands which form part of the marginal

supply of two carpels.

Thus there enter the base of each carpel three main bundles - the midrib and two marginal bundles. The marginal bundles remain distinct throughout their course. As in H. orientalis it is the marginal bundles which give off strands to supply the ovary wall, the midrib remaining unbranched. Although there is agreement in this point the method of branching of the secondary vascular strands and of the vascular supply to the style are entirely different.

From the transverse sections it was found that in this species there were no bundles flanking the midrib, due to the fact that the lateral branches from the commissural strands either fuse directly with the midrib or do so after running parallel to it for a short time. As the apex of the loculus is reached, it was found that the xylem elements in the marginal bundles die out for a short distance, only for the lignification to reappear at a higher level. The number of vessels in the marginal bundles at this level is less than in H. orientalis.

At the base of the style there are present five bundles, the midrib, a strand on either side, and the

two marginal bundles. The bundles flanking the midrib are branches from the marginal bundles, which have been given off at a lower level. This condition persists for some distance up the style. Gradually the branches from the marginal bundles approach the midrib and fuse with it. (See fig. 31 A). There is thus a solid arc of xylem in the position of the midrib. The bundles remain thus until almost the apex of the style. Here the marginal bundles pass round and fuse with the compound midrib bundle, so that there is a semi-circle of xylem vessels in the style. These all end abruptly below the stigmatic surface. It will be noted that, as in H. orientalis, there is only a small amount of phloem, and that this is associated with the midrib bundle.

The details of the branching of the secondary supply to the carpellary wall were studied from the mounts of whole carpels. Fig. 27 A - C shows the main characteristics of the venation of the carpellary wall in this species, and are strikingly different from the other species. The number of branches given off by the marginals varies considerably. In some cases only ten main branches were given off, while in others twenty were found to be present. These strands branch frequently and

anastomose. Branching may occur as the strands leave the marginal bundles, near the midrib, or at any point in its course round the carpellary wall. In general, the secondary strands developed near the base of the carpellary wall tend to branch less frequently than those given off at a higher level. In the upper third of the carpel wall the lateral strands branch frequently and anastomose, so that the wall is closely veined. The lower branches of this system tend oto curve downwards, the central ones pass straight out, whilst the higher ones curve upwards, thus dividing the carpel wall into three main divisions.

It will be seen that many of the branches end blindly in the carpellary wall, particularly the shorter ones which fail to anastomose. Near the midrib the strands tend to become more branched, and of these only one or two fuse with the midrib. Near the apex it will be seen that a branch of the last lateral from each of the marginal bundles enters the base of the style. In fig. 27 C, however, it is a strand given off at a lower level which passes up and enters the stylar region.

HELLEBORUS VIRIDIS.

In this species the number of parts in the gynoecium varies from three to four carpels, there being normally four present. This species is thus intermediate between H. orientalis and H. foetidus. Here the flower stalk is covered with hairs, but they do not possess the swollen head which was characteristic of H. foetidus. No glandular hairs occur on the carpellary wall, but in some flowers there were small crescentic pits, the epidermal cells of which appeared to be of a glandular nature.

Here, as in the other species, just below the region of departure of the perianth traces, the flower stalk contains ten bundles arranged in a ring. Of these five are radially elongated, and pass out to supply the perianth segments. These divide as in the other two species, the primary division being into three, the midrib remaining unbranched, whilst the marginal bundles usually divide once, so that there are again five strands entering the base of each perianth segment.

The method of division of the tangentially elongated bundles is remarkably different from the other two species studied. Here, after the division of the bundles of the pedicel into two main types, the xylem vessels in the tangentially elongated

bundles end abruptly, so that there are no lignified elements in these bundles at the level shown in fig. 32A. This condition persists for some time, the position of the bundles being indicated by the the phloem elements. Fig. 32B shows the appearance of the receptacle at the point where the vascular bundles again contain the lignified elements. It will be seen that the bundles have expanded in a tangential direction, and that the vessels are in small scattered groups, and occupy a different position than at a lower level. These strands continue to become divided up into smaller portions, pass out tangentially and thus fill the gaps caused by the departure of the perianth traces.

One flower, however, presented an entirely different appearance at this level, as is shown in fig. 32C and D. Here, instead of the lignified elements failing to be present in the tangentially elongated bundles, the amount of xylem increased, owing to the activity of the cambium, so that here these bundles are well developed. These bundles continue to expand (fig. 32E and F) and begin to to become divided into a number of smaller bundles. Above this level the perianth gaps begin to close, and the strands which pass out to supply the first

formed nectaries can be seen. (See fig.32G). Each nectary receives a single trace. After the departure of all the traces to the nectaries, the supply to the staminal whorl is given off. One trace enters each stamen. After numerous traces have been given off, the receptacle becomes narrower, and contains fewer bundles.

Diagram XII is a reconstruction of the course of the vascular bundles above the level of the last stamen traces. Fig.33A to C represents this reconstruction in transverse series at various levels. Fig33A shows the arrangement of the bundles in the receptacle at the level where the last of the stamen traces are departing, and can be seen passing out through the cortex. There are also two midrib bundles still within the main ring of vascular tissue - bundles 6 and 13. In this particular flower there are four cappels developed. Ir will be seen from a consideration of the reconstruction that, in the case of carpels, a single receptacular strand divides into two, part passing out as the supply to the midrib of a carpel, and later the remaining portion, after fusion with another receptacular bundle or bundles becomes the supply to one margin of that carpel.

In the case of the other two carpels, a single receptacular strand divides into three portions, the central one becoming, at a higher level, the midrib of a carpel. The other two strands fuse almost immediately with neighbouring bundles, and form the marginal supply to the respective carpels at a higher level.

The midrib always passes out through the cortex and carpellary base without branching. The receptacular bundles, just as they become orientated may give off a small strand, which enters the carpel base previous to the main supply - as is shown in diagram XII. These pass either out through the carpellary base, or curve round the wall and end blindly. In one case, a branch from bundle 12, a strand passes towards an adjacent receptacular bundle, but does not fuse with this although approaching it very closely. This strand later enters the base of the carpel, and fuses with the midrib, which is running out through the base. These small strands may not be given off, but when they are, in no way compare with the well developed bundles in H. orientalis. The whole of the vascular tissue left in the repeptacle after the departure of the midribs, and the small traces, if any, enters

the margins of the corresponding carpels.

In this pith there is no active cell division and thus resembles H. orientalis. It differs, in that the strands which arise sometimes from the marginal bundles are small and fail to reach the midrib tissue. In this respect the condition is more comparable to that found in H. foetidus.

As the marginal bundles enter the base of the carpel in two out of the four carpels fusion of these bundles occurs. This is very complete, so that there is a solid circle of xylem vessels surrounded by phloem. In another case the xylem bundles in carpellary base approach one another very closely, coming into contact at one point, but retaining their individuality, and separating more widely at a higher level. In the remaining carpel the bundles do not come into contact as they enter the carpel base, and remain apart, not fusing at any point in their course - see fig.32C. From these bundles previous to the insertion of the first ovule, strands pass out round the ovary wall. The fused bundles divide into two, and come to occupy a marginal position in each carpel. The carpels soon become free, and the margins are delimited.

Strands continue to pass out from the marginal bundles, curve out round the carpellary wall, and fuse with the midrib.

Diagram XIII, is a reconstruction of the vascular supply to the carpels of another flower. In this only three carpels were present. Here, a receptacular bundle divides into two or three, one part passing out as the midrib, and the remaining parts forming part, if not the whole, of the marginal supply. As the receptacular bundles become orientated a small strand may pass out and end blindly in the carpel wall. As the marginal bundles enter the carpel base they fuse, so that a single concentric bundle enters the base of each carpel, and occupies a central position. Again each single strand divides into two, and above this level separation of the margins occurs.

Thus, at the base of each carpel there are present two marginal bundles and a midrib, in this species not accompanied by any flanking strands, The strands which pass out from the marginal bundles appear to fuse with the midrib directly. Owing to insufficiency of material it was not possible to trace in detail the venation of the wall

The number of lignified elements in the marginal bundles decreases as the apex of the loculus is reached. Above the level of the last ovule there are no vessels present. The midrib at this point is a single bundle, and contains many vessels. It is not until within the base of the style that vessels again appear in the marginal position. In the midrib division has occurred, so that there is a central portion and on either side a group of vessels. Thus the bundles in the style although presenting a similar appearance to those of H. foetidus, differ in that the bundles on either side of the midrib are derived from the midrib itself, and not from the marginal bundles as in the other case. Slowly the marginals approach the midrib and there is formed a solid arc of xylem vessels near the apex of the style. These die out previous to the formation of the stigmatic surface.

COMPARISION AND SUMMARY OF THE THREE HELLEBORUS SPECIES.

In all three species, in the flower stalk, there are five radially and five tangentially elongated bundles, each of the former giving rise to the vascular supply to one perianth segment. The behaviour of the remaining five bundles differs in the various species.

(1). In H. orientalis at first a system of cortical concentric bundles is formed, disintegration of these occurring at a higher level, the vessels passing back into the main vascular ring, but a small strand being left in the cortex, which passes out as a trace to a nectary. In the vascular ring there are now two bundles in place of the one tangentially expanded bundle.

(2). In H.foetidus as a result of the tangential expansion of the bundles, there is a series of concentric bundles all lying in the main vascular ring. Theseconcentric structures break down, accompanied by still further tangential expansion, so that the perianth gaps are closed. It is from this system that the traces to the nectaries arise.

(3). In H.viridus two main types are to be found.

(a). The lignified elements fail to be developed in the bundles for some distance, and on reappearing the vessels are in

several small isolated groups.

(b). Due to cambial activity there appears to be an increase in the amount of xylem in the bundles. Tangential expansion occurs with separation of small bundles, until the perianth gaps are closed.

Here, there is no formation of pseudo-concentric bundles.

The fundamental carpellary supply in all species examined is similar. A single bundle may divide to supply the threeparts of the carpel, or a single strand may supply the midrib and one margin of the carpel, while another receptacular bundle supplies the other margin of that carpel. In no case did three separate bundles supply the midrib and each margin. Fusions may or may not occur between the receptacular bundles.

In H.orientalis and H.viridus the marginal bundles fuse either within the cortex or within the carpellary base, to form a single concentric bundle with the phloem surrounding the xylem. In both species the marginal bundles may remain separate and never fuse. In H.foetidus in the material examined the marginal bundles never fused.

The receptacle, however, presents striking

differences in the three species, due to the variation in the number of carpels formed, and the behaviour of the receptacular bundles. In H.orientalis the last five or six stamen gaps fail to close. From the two bundles opposite the base of each carpel a well defined strand passes out and comes to lie along side of the midrib, but does not fuse with this. When these traces are given off the midrib may be in the cortex or within the base of the carpel. In H.viridus the last three or two gaps of the stamen traces fail to close. Small branches are given off from the bundles opposite the base of each carpel, but this is not of constant occurrence. These are very small and fail to reach the midrib tissue, ending blindly in the carpellary wall. In H.foetidus, failing the development of groups of meristematic cells the stamen gaps do not close and there are no primary traces given off. If groups of meristematic cells arise in the pith they pass out and close the stamen gaps, and also come to lie on either side of the midrib gaps, this tissue entering the carpellary base previous to the main marginal supply.

In all three species the supply to the wall of the carpel is derived solely from the marginal bundles. In H.orientalis as these secondary traces approach the midrib they turn at right angles to their course

and form a flanking system on either side of the midrib. In H.foetidus these bundles fuse directly with the midrib, and this appears to occur in H.viridus also.

Above the level of departure of the last funicular trace the vessels fail to be developed in the marginal bundles but reappear again at a higher level. This unlignified tissue exists for a considerable distance in H.viridus.

The stylar supply differs in the three species.

(1). In H.orientalis at the base of the style there are five bundles, the midrib, the two marginal bundles and two branches from the latter. The marginal bundles fuse with their branches, and at a higher level with one another thus forming an arc of vessels surrounding the stylar canal.

(2). In H.foetidus again five main bundles enter the base of the style, but in this species the lateral branches from the marginal bundles fuse with the midrib, and it is only at the apex that the marginals fuse with the midrib.

(3). In H.viridus there are five bundles at the base of the style but here it is the midrib which divides and gives off two branches.

The marginal bundles very slowly approach the midrib, which has again become a single structure, so that there is a single bundle below the stigmatic area.

Within the style the phloem is not present in the marginal bundles or its branches, and only a little ispresent in the midrib, but this dies out at a higher level, only vessels being present in the upper half of the style.

ERANTHIS.

In this genus two species were investigated, namely:-

(1). Eranthis cilicica.

(2). Eranthis hyemalis.

In both the perianth segments alternate with one another, and with the honey leaves. The stamens tend to be arranged in oblique rows, while the carpels may, in some flowers, be arranged in two alternating whorls, although normally in a spiral.

Surrounding each flower, there is a three leaved involucre of bracts. The flower itself consists of six yellow perianth segments, six honey leaves, six rows of obliquely arranged stamens, whilst the gynoecium consists of carpels, varying in number from three to twenty. These are all shortly stalked. In E. cilicica glandular hairs are present on the wall of the carpel. (See fig.37E).

Eranthis cilicica.

A transverse section of the flower stalk, a short distance below the region of departure of the bract traces, shows a ring of bundles of varying

sizes surrounding a hollow pith. (See fig. 34A). Six large vascular bundles are present placed equidistant form one another , and between these numerous smaller bundles of varying sized occur, the central one of which tends to be larger than the others. On either side of each large bundle, there is a small accompanying strand. (See fig. 34A, B, and C). Fusions occur between the small bundles, so that , just below the region of formation of the bract traces, three intermediate strands are to be found.

It is the six large vascular bundles which become the traces to the bracts. These may divide while still within the ring of bundles, or on their outward passage through the cortex. Three of the large bundles pass out, each of which becomes the midrib of a bract. The remaining three bundles give rise to the marginal traces. Each bundle divides, one part forms the supply to one margin of a bract, the other portion supplying the margin of adjacent bract. Thus one whole and two half bundles supply each bract of the involucre. (SEE fig. 34C).

In some specimens examined, seven large bundles were present in the pedicel, so that, in

one case, two separate bundles supplied adjacent margins of neighbouring bract segments, and not a common strand, as in the other two bracts.

The intermediate bundles have already commenced to divide into a number of smaller bundles, and from these arise the traces to the perianth segments. One two or three gaps may arise in the stele as a result of the departure of the traces to each segment. Three stelar bundles are normally involved in the supply to one segment, the whole, or part only, becoming a trace. Fig. 34 D illustrates a flower, in which, traces are running out to three perianth segments, one, two, and three gaps arising in the stele, as the result of the departure of these traces. Division of the marginal bundles may occur in the cortex, while division of the midrib is not of frequent occurrence. The perianth supply is thus similar in many respects to that of Caltha.

After the departure of the perianth traces, the supply to the honey leaves is given off. A receptacular bundle may divide into two or three parts, one of which becomes a trace to a nectary. In a similar manner the traces pass out to the stamens.

The carpellary supply is illustrated by diagram XIV and figs.35A to D, also diagram XV with fig.36A to C. The one flower contains nine carpels, while in the other twenty five are developed.

From a consideration of diagram XIV, it will be seen that there is variation with regard to the behaviour of the bundles above the level of departure of the last stamen traces. Division of many of the receptacular bundles occurs a considerable distance before their outward passage as carpellary traces. It will be seen from fig.35C, that opposite the apparent base of insertion of each carpel, there is present a single vascular bundle, the whole of which later passes out as the midrib of the corresponding carpel. The bundle passes out without branching, either within the cortex or carpellary base. A single receptacular bundle may give rise, not only to the midrib, but also to the supply to one margin of that carpel. This condition is seen in diargam XIV, bundle 9. In many cases, however, this remaining strand divides to supply one margin of two carpels - as in the case of bundles 8 and 12. Fusions may occur between receptacular bundles, lying between the midrib gaps, previous to their outward passage as

marginal bundles, again each dividing to supply one margin of two carpels.

In diagram XV more frequently a single receptacular strand, without previous division forms the midrib bundle of a carpel. In one case, bundle 18, a single strand divides to form the midrib and the marginal supply of a carpel. In this particular carpel, only two bundles enter the pedicel, division of the larger one occurring at a higher level within the pedicel, so that the three main traces are present at the level of the loculus. Two carpels are formed at a very much higher level than the other carpels - see fig.36C. The traces to these arise from receptacular bundles, which, at a lower level, have given off marginal traces to the first formed carpels. (See fig.36 and diagram XV, bundles number 4 and 6, also bundles 10, 12 and 15). This offers a parallel to the condition obtaining in Trollius, where the receptacular bundles give off traces to the first formed circle of carpels, later to the second, and finally enter the later formed carpels, occupying a midrib and marginal position. It is of regular occurrence in this genus, but in Eranthis is an isolated example.

To form the marginal supply a single bundle between the midrib gaps, divides to supply one margin of two adjacent carpels. This is of regular occurrence when three bundles enter each carpel.

In three of the fifteen carpels, only two bundles enter the base of each. In these cases the intermediate bundle between the midrib gaps fails to divide, the whole entering the base of one carpel ; e.g. bundles 20, 16. 24. A single bundle forms the whole supply to one carpel. (See fig. 36A to C, bundle 19).

Thus one two or three bundles may enter the base of each carpel. Within the pedicel division occurs, so that, when the level of the loculus is reached, three strands are present.

From the serial sections it was observed that the main supply to the ovary wall was derived from the marginal bundles, and that these secondary strands did not fuse with the midrib. In some it was seen that within the pedicel one, or two, branches were given off from the midrib bundle, and that these formed the first branches in the wall above the level of the loculus.

Fig. 37A and B, show the relative size of the midrib and marginal bundles in a fully developed flower. It will be noted that the midrib contains about the same number of vessels as the marginal bundles.

The venation of the carpellary wall was investigated from cleared preparations of whole carpels. Fig. 39A and B illustrates the course of the secondary system of bundles in the carpels. Branches may or may not be given off by the midrib bundle, but when present, forms the first branch in the carpellary wall. In all cases it arises in the pedicel. It may be :-

(1) relatively short, failing in a few cases to reach the expanded wall of the carpel,
(2) pass out round the wall without branching,
(3) may branch several times.

This branch from the midrib never fuses with any lateral branches from the marginal bundles.

The main secondary supply, however, arises from the marginal bundles. These give off varying number of branches to the wall of the ovary. The laterals tend to branch frequently, as they pass out towards the midrib tissue. Anastomosis is of relatively rare occurrence, the branches from one

main lateral remaining independent throughout their course. The laterals approach the midrib bundle but never fuse with it. Some may curve round sharply at right angles and run parallel for a short distance.

At the base of the style the marginal bundles end abruptly. No laterals from the these bundles enter the stylar canal, the midrib alone forming, in all the specimens examined, the entire vascular supply. This latter remains unbranched, and ends blindly just beneath the stigmatic surface. Fig. 37D shows the midrib bundle near the apex of the style, as a single strand consisting mainly of xylem vessels.

ERANTHIS HYEMALIS.

This species differs from the preceeding, in that, the number of carpels in the gynoecium tends to be reduced in number to six or seven.

The arrangement of the bundles in the flower stalk , below the region of formation of the perianth traces, is similar to that of E. cilicica. Six of the large vascular bundles give rise to the bract supply, sometimes seven, and divide in a manner similar to the preceeding species. In the perianth supply there are remarkable differences. Again, after the departure of the bract traces, the intermediate bundles divide into a number of smaller bundles. In this species, five, seven, or nine gaps may arise in the relation to the supply to one perianth segment. Again division of the bundles may occur in the cortex.

After all the traces have passed out to the perianth segments, the vascular supply is given off to the honey leaves, and the stamens. these arise in the same way as in E. cilicica.

Diagram XVI with fig.38, and diagram XVII,

illustrate the vascular supply to the carpellary whorl in two flowers, one of which possesses six, the other seven carpels.

Diargam XVI shows that a single receptacular bundle passes out to become a carpellary midrib. Only in one case is there division of a bundle, one part becoming the midrib, the other portion forming, at a higher level, part of the supply to one margin of that carpel. There may be one, two, or three bundles between the midrib gaps. Fusion of these strands takes place, so that, there is only a single bundle between the gaps. These divide equally into two, each part supplying one margin of two adjacent carpels. In all the other carpels of this flower, three separate strands enter the base, the midrib and the two marginal bundles.

In diagram XVII, one additional carpel is formed, but this is not associated with an increase in the number of bundlesiin the receptacle after the departure of the stamen traces. In two carpels the midrib arises from a bundleswhich divides and supplies also two margins - adjacent margins of neighbouring carpels. (See diagram XVII, bundles 5 and 10). One or two bundles may lie between the midrib gaps, and in the latter case, the bundles

fuse to become a single strand. Division of these single strands takes place, the two resulting strands passing out to form part of the marginal supply of adjacent carpels.

Thus in this species, in the flowers examined three separate strands enter the base of each carpel. In no specimen did the marginal bundles of a carpel fuse. All the vascular tissue, as in the other Eranthis species, was used up in the formation of the carpellary traces.

Examination of the secondary vascular supply to the carpellary wall showed that this exhibited the same type of venation as in E. cilicica, namely the presence or absence of the branches , or branch, from the midrib, arising within the pedicel, and forming the first branch in the carpellary wall, the frequent branching of the secondary vascular bundles, infrequency of anastomosis, failure of the laterals to fuse with the midrib, and the midrib alone continuing in the style, the marginals ending abruptly at the base of the style. These various features are illustrated in fig.40.

Thus the two species are similar as regards the vascular supply to the various whorls, excepting

the perianth supply. In E. cilicica only three gaps are caused by the departure of the traces, whereas in E. hyemalis five or more gaps occur. A larger number of traces enter the base of each segment in the latter. The origin of the carpellary traces is very similar in the two species. Compare diagrams XIV and XV, with diagrams XVI and XVII.

From the various flowers examined we may conclude that the basic type is where a single bundle supplies the midrib, and the two receptacular bundles between the midrib gaps fuse for a short distance, later divide, and supply one margin of two adjacent carpels. As a result of the increase in the number of carpels, various modifications of this are to be found. They may be briefly summarised as follows:-

(1). A single bundle supplies the midrib, but only one bundle is present between the gaps, and this divides to supply adjacent margins of neighbouring carpels.

(2). A single bundle supplies the midrib, and also the two adjacent margins of neighbouring carpels.

(3). A single bundle supplies the midrib, and one margin of that carpel.

(4). A single bundle supplies the whole carpel. Division of a receptacular bundle occurs, at a higher level, part of the bundle becomes the midrib, and later the remaining portion enters. Division of the larger bundle occurs within the pedicel.

(5). A single bundle supplies the whole carpel, but in this case, enters as a single strand.

(6). A single bundle supplies many carpels. This occurs when a second circle of carpels is formed, a receptacular strand dividing to supply both whorls.

CIMICIFUGA

Two species were investigated, anatomically, in this genus.

(1) Cimicifuga davurica

(2) Cimicifuga racemosa

The flower consists of four or five white perianth segments, followed by an equal number of honey leaves, a great many stamens, spirally arranged and in C. davurica, the gynoecium consists of normally five carpels, but the number may range from two to six. In the other species, however, only a single carpel is present. The carpels in the former species are all shortly stalked. Hairs are present on the carpellary wall in both species, as well as on the flower stalk and part of the receptacle.

Cimicifuga davurica

There is variation with regard to the arrangement of the bundles in the peduncel. In some stalks sclerenchyma was found to be associated with the bundles, whilst in others, this was absent. Where sclerencyhma was developed, as the level of departure of the perianth traces is reached, the thickening ceased to be laid down on the cell walls.

A. No sclerenchyma present

In this type, five bundles were found to be present in the peduncel, arranged in a ring surrounding a solid pith. As we pass up the stalk

towards the base of the receptacle it was found that the bundles divided, so that there were seven to ten bundles at the level of departure of the perianth traces.

B. Sclerenchyma present.

Two types were found, as illustrated in Fig. 41 A and B. Fig. 41 A is similar to the above type, but with a ring of sclerenchyma, broken at two points, surrounding the bundles. There are sclerenchymatous indentations which separate the bundles. In Fig.41 B, there is a complete ring of sclerenchyma, with numerous indentations. The stele consists of about ten separate bundles, separated by the sclerenchyma. In this latter type, the bundles, without previous subdivision, give rise to the traces of the perianth segments. In the former type however, the bundles, after the disappearance of the sclerenchyma, form two arcs of vascular tissue - the individual strands having fused with one another on either side of the gaps. It is as a result of the departure of the perianth traces that the stele becomes dissected.

Part of a bundle, occasionally the whole, leaves the main ring of vascular tissue, passes straight out through the cortex, and enters the base of a perianth segment. Division occurs within the

base, giving rise to a midrib and two marginal bundles. There is no further subdivision of these bundles.(See Fig.41 C). In a few cases, prior to entering the base of a segment, division occurred, so that three separate strands entered the base of each - i.e. division occurred in the cortex instead of within the base of the segment. Three or four other such traces arise, and pass out to the remaining segments.

As a result of the departure of these traces the stele has become further divided into smaller bundles, and numerous fusions occur. Traces how pass out to supply the nectaries and stamens, one trace entering the base of each. These traces are given off in rapid succession, the gaps being quickly closed by division of adjacent receptacular bundles.

The gaps continue to be closed, until the last two, which normally fail to close. In some specimens examined, the last three or four gaps never closed, whilst in others the last two or three gaps closed, and the gaps of stamens traces given off at a lower level remained unclosed.

To consider the normal type in which there are two gaps, and five carpels developed. On either side of these two stamen gaps, the bundles are so close

together, that it is impossible to distinguish separate strands. Thus we have two solid arcs of vascular tissue. From these, individual strands take shape at a slightly higher level, usually five in number, three on one side and two on the other side of the gaps. Each passes out immediately and enters the pedicel of a carpel, becoming concentric within the base of this. Fig. 42A shows a peculiar arrangement of the bundles, three entering the pedicels, whilst two bundles have passed into the centre of the receptacle, and enter the pedicels developed, at a higher level in this position.

When six carpels are developed, each arc of vascular tissue may divide into three separate strands, each of which enters the base of a pedicel - see fig. 42B. A concentric bundle passes in towards the centre of the pith, to supply a carpel developed in this position. Fig. 42C shows a variation of this type. Bundles 1,2,3 are derived from the one arc of vascular tissue between the two gaps, and bundles 4,5,6 from the other. From the one gap four bundles are derived, for as bundle 3 starts to pass out, a strand becomes detached, which passes in towards the centre of the pith. At the same time, one of the other bundles of the ring of tissue, bundle 2, passes

in towards the centre also. These two bundles meet to form a single concentric strand in this position. At a higher level, this bundle enters the pedicel of a carpel. Figs. 42 D to F show the division of the bundles to form the supply to six carpels, where the last few stamen gaps are closed. Again a bundle occupies a central position in the pith.

In another flower, only three carpels were developed. In this type, the last three gaps failed to close, and the intervening vascular tissue passed out as a whole, in each case, to supply a carpel.

Thus a single concentric bundle is present at the base of the pedicel of a carpel. At the top of this short pedicel, the central portion of each strand runs out to become the midrib of the carpel, the two remaining portions becoming the two marginal bundles. At a slightly higher level the loculus is developed and the margins become delimited.

From the serial transverse sections it appeared that the secondary vascular supply in the carpellary wall was derived from the marginal bundles, although occasionally in some flowers a branch was given off from the midrib. As the style is approached the marginal bundles commence to pass round towards the midrib. Within the style the bundles fuse to form

a single arc of xylem , with a little phloem present over the midrib, surrounding the stylar canal. In Fig. 43A one marginal bundle has fused with the midrib, whilst the other is approaching it.

From the mounted specimens of whole carpels (see Fig. 44A - C) it was seen that the main lateral supply in the carpellary wall is derived from the marginal bundles, but that the midrib may give off one or two branches which pass out for a short distance into the carpel wall. This position of this branch is variable. The branches from the marginal bundles are relatively few, and usually entirely unbranched, but may fork at the end distant from the margin. Anastomoses is of a rare occurrence. The last lateral branch from the marginal bundle may enter the style and fuse with the marginal bundle.

CIMICIFUGA RACEMOSA

The flower in this species differ from C. davurica mainly in possessing only one carpel.

The flower stalk contains six or seven large vascular bundles arranged in a ring surrounding a solid pith (see Fig. 45A). No sclerenchyma was found to be present in the peduncel of any flowers in this species. Without previous division a whole or a part of a bundle may pass out to become the supply to a perianth segment. As in C. davurica a single trace passes out through the cortex, and within the base of the segment, the trace divides into three separate strands. In a few cases, the trace divides within the cortex, so that three separate strands enter the base of each segment (see Fig.45B). In one specimen three separate bundles gave off a trace, and entered the base of one segment. As the perianth supply is being given off, there is at the same time division of the receptacular bundles, so that numerous small strands result. These approach one another and sub-divide, thus forming an almost solid ring of vascular tissue. From this the supply to the honey leaves and the stamens arises, one trace entering the base of each (see Fig. 45C). The stamens form a very low spiral and are given off in rapid succession. The gaps are closed immediately

after the departure of the stamen trace. It would appear that part of a bundle may pass out into the cortex, and divide to supply two or more stamens (see Fig. 46A).

Gradually the receptacle becomes narrower, after the majority of the stamen traces have been given off. Up to the level of departure of the last few stamen traces all the flowers sectioned present a very similar appearance. Above this level, however, the bundles exhibited numerous differences.

Firstly, the actual number of bundles left in the receptacle after the departure of the last stamen trace varies considerably, and it is difficult to establish a basic type. It would appear, however, that, most frequently, five bundles are present, three of which are large and two small - small parts of bundles, the major part of which have passed out to become stamen traces.

These small strands link up with any of the three large bundles present, the two strands freqently fusing with the same bundle. One of the bundles may have commenced to pass out through the carpel base before the strands fuse with the remaining bundles.

The following types were also found:-

(1) Three large bundles and one small strand. This was of frequent occurrence.

(2) Four bundles of almost equal size, but in some cases, two of which tend to be slightly smaller than the other two.

(3) Four large bundles and one small strand.

(4) Six bundles, three of which tend to be large, two very small remaining parts of a bundle, the major part of which have become stamen traces, and another bundle of intermediate size.

Again, as in the type described above, the small bundle or bundles fuse with an adjacent large bundle, or in the case of (2) and (3), the two slightly larger bundles fuse, or two of equal size. In one specimen, the small strand ended blindly in the receptacle. In another flower, the intermediate strand passed out, as the first branch in the carpellary wall, without fusing with an adjacent strand.

Thus, normally, at the apex of the receptacle, previous to the outward passage of the midrib, there are three bundles present, but occasionally four are formed. A bundle previous to passing out as the

midrib may divide, a portion remaining in the receptacle. At other times only the central portion of a bundle may pass out to become the midrib. The behaviour of the remaining portion or portions is variable. In some specimens they pass back and fuse with the marginal bundle or bundles directly. In other cases, the strand or strands may divide and give off branches to the carpellary wall, as the main portion passes back towards the marginal bundle. Instead of fusing with the marginal bundle, the strand may come to lie between the marginal bundles and there end blindly. The latter type is illustrated in Fig. 47 A - C and here also, as the midrib bundle was passing through the carpellary base, it also branched.

As the midrib is running out through the carpellary base, portions may be detached from the marginal bundles, which pass out as one of the first branches in the carpellary wall.

These three main bundles - the midrib and the two marginals, enter the base of each carpel. The midrib as it passes out through the carpellary base, may give off a branch on either side. This is the only branch given off by the midrib, the whole of the second vascular system of the carpellary wall, apart

from this one branch, being derived from the marginal bundles.

These facts, established from transverse serial sections were confirmed by examination of the mounted specimen of the carpel, Fig. 48A - C. The number of branches given off by the marginal bundles varies as does also the mode of branching of these lateral bundles. Division may occur just as the lateral branch leaves the main bundle, or at any point in its course round the wall, but is most frequent in that part of the wall nearest to the midrib tissue. Anastomoses may or may not occur (Compare Fig. 48B & C). It will be seen from the figures that these lateral bundles all end blindly in the carpel wall, not fusing with the midrib bundle. At the base of the style the marginal bundles fork repeatedly, but all the branches end blindly in the stylar tissue, the midrib alone continuing to the apex. This bundle remains unbranched. Within the style it becomes more heavily lignified. Figs. 43B & C show the midrib, near the base of the style and within the style. It will be noted that the bundle has expanded laterally, there being no phloem present opposite the extension on either side.

XANTHORHIZA APIIFOLIA

The genus Xanthorhiza contains only the one species - X.apiifolia, the flowers of which are very small. The parts are arranged in alternating whorls - five perianth segments, five honey leaves, ten stamens and ten carpels. The number of stamens and carpels, however, is variable, the parts in the gynoecium varying in number from four to sixteen. The carpels, as in Cimicifuga davurica, are all shortly stalked. Within each carpel there are a varying number of ovules, many of which are sterile.

In the peduncel, there are five bundles, arranged in a ring surrounding a solid pith. Over the phloem in each bundle there is an arc of sclerenchyma. There a few of the bundles are large, whilst one or two are much smaller (see Fig. 49A). As the level of departure of the perianth traces is reached, either of the following conditions is found to occure:-

(1) Each large bundle, without previous division, gives off three traces to the corresponding perianth segment - a midrib and two marginal bundles. The central part of each bundle is normally involved in perianth trace formation (see Fig. 49B) so that two small strands are left in the receptacle, after the departure

of the supply to one segment. Following the outward passage of some of these traces, there are numerous fusions of bundles in the receptacle.

(2) The bundles expand tangentially, divide into numerous smaller strands. Fusions occur and the final result is a solid ring of vascular tissue (see Fig. 49C). From this, three traces pass out to each, leaving five gaps in the ring of vascular tissue.

The supply to the honey leaves and stamens now arise in rapid succession, one trace passing out to each organ, the gap being rapidly closed.

As the apex of the receptacle is reached, a varying number of stamen gaps fail to close. The bundle between two gaps may pass out through the cortex, and enter the corresponding pedicel. In many cases, however, division occurs so that two or three separate strands are given off, each of which enters the base of a pedical (see Fig. 50 A - C). The whole bundle in each pedicel forms the midrib of a carpel. No marginal bundles are present (see Fig.51). The midrib bundle passes up the carpel entirely unbranched, No strands appeared to be given off to supply the ovules or the carpellary wall. The midrib bundle enters the style and persists for a short distance.

DISCUSSION AND CONCLUSIONS

The genera investigated present, morphologically, a wide range of structure - from the assumed primitive type, with a large number of parts arranged spirally - e.g. Trollius, through the hemispiral type, represented by Eranthis, to the truly cyclic type, where the parts are arranged in whorls, with a definite number of constituent parts in each whorl.

From this field, we would expect to be able to establish the changes which occur anatomically, with the development of meristic precision, associated with cyclic structure, and how this is reflected upon the vascular cylinder.

We may consider first of all the supply to the perianth segments, followed by the supply to the honey leaves and stamens, and finally the variations which occur in the supply to the carpellary whorl.

A. SUPPLY TO THE PERIANTH SEGMENTS

In such types as Caltha and Trollius the large vascular bundles expand tangentially, previous to the outward passage of the perianth traces, so that there

is formed an almost complete cylinder of vascular tissue. From this, traces pass out to the segments. In Trollius, the first half of the total number of segments formed received more traces than the second half. In the supply to the former, five gaps are caused in the main stele as the result of the outward passage of the traces to each segment, whilst only three are caused in the later formed segments. Trollius is exceptional in this respect. In Caltha one, two, or three gaps may be caused in the stele as the result of the outward passage of the supply to a segment. This variation in the number of gaps is not related to the position of the segment concerned - e.g. the supply to the first segment formed may leave only one gap in the main stele. As in the preceeding species, the marginal bundles tend to branch on their outward passage through the cortex. In Caltha, however, the midrib bundle may also give off branches. Similar to Caltha, is Eranthis cilicica. Here, of course, the stele is dissected prior to perianth trace formation, due to the division of the bundles to close the bract gaps. E. hyemalis differs, however, in that there are normally five to nine gaps in the stele, in relation to each segment. Any of the traces may branch on their outward

passage through the cortex. From this type we come to consider the Helleborus species, in all of which a single strand, without fusing with other receptacular bundles, divides radially within the main ring into three strands, to form the midrib and two marginal bundles of a perianth segment. Similar to that, is the type which occurs in Xanthorhiza apiifolia, but in this species the bundles may form a solid ring of vascular tissue, previous to the outward passage of the traces. In Helleborus, the marginal bundles each give off a pair of traces, so that five bundles enter the base of each segment. In the Xanthorhiza, however, there is no division of these bundles. The midrib bundles in both genera never give off traces. In an exceptional type of Cimicifuga racemosa, three separate strands, from three separate bundles, passed out through the cortex and entered a perianth segment. In another type, a single strand is given off, by tangential division or a whole bundle may pass out, in both cases, without division, so that a single strand enters the base of each segment. Of fairly frequent occurrence is the branching into three, prior to entering the base. Similarly in C.davurica the two latter conditions are also found - the single trace being

of frequent occurrence.

Thus we have a series established showing the trend of supply, from a three, five, or nine lacunar gap system. to a single gap, in relation to the vascular supply to one segment. Marginal bundles frequently branch on their passage through the cortex. This occurs to a greater extent in such types as Cartha Trollius where there is a large basis of insertion of the segments. Similarly this would appear to be the cause of the branching of the midrib bundle. Apart from this, the supply resembles closely that of a normal foliage leaf.

B. Honey Leaves and Stamens

After the departure of the perianth traces, the stele is dissected into a large number of smaller bundles. From these the supply arise, first to the honey leaves, and later to the stamens. In each case a single trace is given off and enters the base of the organ concerned. There are no exceptions to this in the material examined. Within the base of the honey leaves it was seen that the bundle may divide into three.

C. Carpellary Supply

After the departure of the last stamen trace, the midrib bundles commence to pass out through the

cortex. In Trollius as a general rule, and in Caltha in one type, we find that a bundle passing out through the cortex divides, the central portion becoming the midrib of the corresponding carpel, while the two small strands enter the carpellary base, and come to occupy a marginal position at the base of the carpel. At a higher level, from adjacent strands in Trollius, two separate bundles enter and fuse with the corresponding bundles already present. In Caltha, it is frequently only one strand which enters, and this divides in a complicated manner into two bundles. Thus in this type three five, or four, separate strands entering the base of each carpel, causing three gaps in the main stele, or two in the case of Caltha where only one strand enters as the marginal supply. In the latter species other main types are also found, and a series was established (see page 41.) in which the small strands given off by the midrib remained receptacular, and fused with adjacent bundles, which later formed the marginal supply. Here again there may be only two gaps in the stele as the result of the departure of the carpel traces. Another type is where the receptacular strand supplies all three parts of the carpel, causing three gaps in the main stele. Here, equal division of the receptacular bundles occurs,

the central portion forming the midrib, the bundles on either side of the gap forming the marginal supply. Smith (96) describes as typical of Caltha one separate bundle supplying the midrib of a carpel, and the margins, while only part of the bundles on either side of the midrib gap become carpellary traces. This is of rare occurrence in the material sectioned and is only recorded for one carpel of a flower. In another type a single strand supplied the midrib as well as one margin of that carpel, and the margin of a neighbouring carpel.

Thus we have within one species variation with regard to:-

A. The number of traces entering the base of each carpel
B. The number of bundles involved in this supply.
C. The number of carpels these bundles supply.
D. The number of gaps formed as the result of the outward passage of these traces.

On this basis, would not be justified in interpreting these variations as indicative of a different number of parts in each whorl. Also, where there is a reduction in the number of parts supplying a given number of carpels, a single strand by tangential division may supply

(1). The midrib of a carpel,

(2). One margin of that carpel,

(3). The neighbouring margin of an adjacent carpel.

Another receptacular bundle supplies the other margin as well as a margin of another carpel. On a basis of the carpel polymorphism theory, this particular carpel would be interpreted as $\frac{1}{3}+\frac{1}{3}+\frac{1}{2}$ carpels, which is not equal to two carpels.

To consider Trollius again. The bundles left in the receptacle after the departure of the stamen traces have to supply all the numerous carpels developed. Thus we find radial and tangential divisions of the bundles, part of which pass out to form the supply to the first formed carpels. Similarily, for the second circle developed, and so on until the last whorl. Here, however, the whole may not pass in, part remaining in the receptacle. As a resul t of this, it will be seen that bundles which were originally separated from one another, now, at a higher level, are adjacent and form the supply to one carpel. This same feature is also seen to a certain degree in Eranthis cilicica and also in Caltha where a bundle divided, part passing to form the supply to one margin of a carpel on one side of the receptacle, the other portion similarily supplying a carpel on the opposite side of the recept-

acle. Must we interpret this on Saunder's theory that these two distant margins are each half of the same carpel?

To return to a consideration of the Helleborus species. As in the one type of Caltha, so here also but of more frequent occurrence, is the division of a single bundle within the receptacle to supply all three parts of the carpel. But more often a bundle divides tangentially, the trace evolved forming the midrib. At a higher level, the two bundles on either side of the gap, enter. Would this be intrepreted as the midrib and one margin each being equal to one halh carpel, while the other margin is a whole carpel? In the previous case each part of the carpel was a third of a carpel.

In Eranthis the fundamental supply would appear to be three separate bundles causing three separate gaps in the main stele. But with the remarkable increase in the number the bundles - see Diagram XV and the increase in the number of carpels, this fundamental relationship is upset. Here, within one flower, we have a series of one, two, and three bundles being involved in the supply to one pedicel of a carpel, and causing the corresponding number of gaps in the main stele. Within the pedicel, division

occurs, so that there are three bundles below the level of formation of the loculus. But this variation would not lead us to assume that three different types of carpels were present in one flower.

In Cimicifuga davurica the arcs of tissue left after the departure of the stamen traces, break up simultaneously into several strands, each entering the base of a pedicel. Division occurs within this. Thus we have one gap and one trace entering each pedicel, In Xanthorhiza a similar situation is found, but more complicated, owing to the tendency of the formation of a larger number of carpels. Thus each arc divides into several strands, each of which gives off a carpellary trace, the remaining bundle later entering the base of another carpel. Within the pedicel division does not occur, the whole becoming the midrib of the carpel. The carpel is very small, and it would appear that threr is no physiological need for a vascular supply in the marginal position. But there is no reason to interpret the carpel of this species as being a true valve carpel, while that of Cimicifuga davurica would, most likely, be interpreted as $\frac{1}{2}$, 1, $\frac{1}{2}$ carpels.

This brief review has attempted to bring

out the connecting links between the various genera and species, and to present the type of carpel in Trollius as similar to that in Cimicifuga or Xanthorhiza, and to show that with an anatomical basis, it is not logical to establish a carpel polymorphism theory on the course of the vascular bundles.

An important point to stress is the relationship between the number of bundles in the receptacle, above the level of departure of the stamen traces, and the number of carpels formed. Taking Helleborus orientalis as an example, it will be seen that twelve bundles divide to supply five carpels, and that only ten bundles divide to supply six. In another case fourteen bundles remained after the departure of the stamen traces, and that they gave rise to the vascular supply to the same number of carpels. Thus there is no relationship between the number of receptacular bundles and the number of carpels developed. This can also be illustrated with reference to other genera. But the carpellary number must affect the division of the bundles, and hence the varying number of parts of a carpel, or carpels a single receptacular bundle may supply. The number of bundles left in the receptacle, above the level of departure of the last stamen trace must

of necessity, be affected by the number of stamen traces given off, and to a lesser extent by the number of traces arising below this level. This is another point completely neglected by Saunders.

Reference must here be made to a statement of Saunders, in which she expresses the belief that the only carpel recognised by her as being truly "monocarpic" is tha achene, such as found in the Ranunculaceae and the Rosaceae. Reference need only be made to the statements of Eames and Chute, correlated with the results of this work, which indicate clearly that an achene is a reduced follicle. in which there is a tendency to the fusion of the carpellary traces. A perfect series is presented showing, step by step, how this has been brought about. Even based on the vascular supply, some achenes would be interpreted as possessing $\frac{1}{2}$, 1, $\frac{1}{2}$, carpels, whilst others would be truly one carpel.

Without going into further detail with reference to Saunders thoery, we will now turn to that of Thomas based on a study of the course of the secondary vascular bundles of Caltha, and a known fossil - Gristhorpia. As already pointed out he failed to notice the fact that, very frequently a branch, or branches, arise from the midrib bundle,

passing out for varying distances into the carpellary wall. It is also to be noted that they tend to arise near the base of the carpel. No reference is made to the fact that five separate bundles may enter the base of a carpel. In a later paper he sets forth his nine features which should be studied. Evidently he does not think that "Example is better than precept". Immediately he sets forth his theory on the nature and origin of the cappel without a study of the development of these structures to mention only one important point out of the nine. This might reveal some interesting facts with regard to the lateral stigma of Drimys, and the supposed change to a terminal position in such types as Caltha.

Directly opposed to this theory is that of Thompsom. At this stage of its development , the theory seems rather fantastic, but shows that attention should be drawn to the facts of development. Something may be gleamed from this as to the nature of the carpel, and may act as a corrective to the overspeculation of some other authors. It will be interesting to await the results of a study of the development of a female unisexual flower.

The leaf theory of Goethe would now appear to

be attacked from every possible angle - the development (Grégoire and Thompson), the vascular supply to the organ (Saunders), the vascular supply within the carpellary wall, and the relation of this, to what is considered, as now, the nearest Angiosperm amoungst fossil records, - Thomas.

As regards basing a theory on the vascular supply - the origin and number of traces, this work proves the plastic nature of the vascular system. The fundamental supply resembles that of a leaf. Adhesions and adnations within the receptacle must be considered. In this, the primitive types, the variation within the secondary vascular supply to the carpellary wall is most obvious. Within one flower, there may or may not be branches arising from the midrib, but particularly with reference to the stylar supply. The function of the vessels, here, would appear to be to keep the stylar canal moist for the germination of the pollen grains, and that any of the three bundles may be able to supply this need. In types such as Trollius and Caltha we find this variation with regard to the bundles supplying the style, but in the Helleborus species, each has solved the problem in its own way, but the final result is an arc of vascular tissue surrounding the stylar canal.

At the present time, with the fossil record of one primitive Angiosperm, it seems rather rash to base a whole theory around this structure. Let us record, in detail, the various points from our most primitive types of our present day Angiosperms and await, with patience, the discovery of some of more advanced type of Angiosperm from the fossil records, which may then elucidate our facts.

SUMMARY.

1. There is variation with regard to the number of bundles supplying each perianth segment, and the number of gaps formed. There is a tendency to reduce the number of gaps, and the number of traces entering the base of each, as we pass from the type with a large base of insertion, as in Trollius, to a type with a marrow base, as in Cimicifuga. The marginal bundles frequently branch on their outward passage, and also, occasionally, the midrib bundle. Apart from this branching in exceptional cases, the supply, fundamentally , resembles that of a leaf.

2. The honey leaves and stamens each receive a single strand.

3. In the carpellary supply, there is variation with regard to :-

   a. the number of bundles entering the base of a carpel.

   b. the number of receptacular bundles from which these traces are derived.

   c. the number of carpels each receptacular trace may supply.

4. There is no correlation between the number of bundles in the receptacle, above the level of

departure of the stamen traces and the number of carpels developed above this level.

5. As a direct result of this, the degree to which these stelar bundles are divided, and the number of carpels developed which they supply, must depend upon the number of receptacular bundles, and the number of carpels developed. Thus, a comparatively small number of bundles must divide to a greater extent to supply a given number of carpels, than if a larger number of bundles were present, and vica versa.

6. The whole of the stelar vascular tissue may or may not be used up in the formation of the carpellary traces, Both conditions may be found to occur in the one species - e.g. Caltha.

7. There may be three or five traces enter the base of each carpel - e.g. in Caltha, Trollius, and Eranthis, where the midrib bundle divides in the pedicel, which is considered as an extension of the receptacle.

8. The secondary vascular supply within the carpellary wall varies within fairly wide limits for each species.

9. The main supply to the carpellary wall is, in

the majority of species, derived from the marginal bundles, which give off branches. The terminal endings distant from the marginal bundle, either fuse directly with the midrib or end blindly in the carpellary wall. This is constant within a species.

10. Branches may or may not arise from the midrib bundle within the carpel itself - e.g. Caltha and Cimicifuga davurica. Where present there is a tendency for these bundles to arise towards the carpel base, and pass out into the wall for varying distances. Normally they are not well developed. In Trollius, two branches constantly are given off, which continue parallel to the midrib. Again they tend to arise near the base of the carpel.

11. These facts may be taken as support of the view that the primitive carpel may have been a palmately veined structure.

12. The stylar supply, in the species where the number of parts in the gynoecium tends to be constant, is, of itself, constant. In Trollius and Caltha there is variation , the midrib, or marginal bundles, or both may supply the style.

This variation also occurs with one gynoecium.

13. The fundamental vascular supply to a carpel is similar to that of a leaf. The venation within the carpellary wall, however, does not resemble that found in a true leaf.

14. These results do not lend support to the theory of carpel polymorphism, nor do they justify Thomas' interpretation of the probable origin of the carpel in such a type as Caltha.

15. The present state of our knowledge of ancient Angiosperms, and of the more primitive types in our present day flora, only suffice to show the tremendous gap in our knowledge of the probable primitive Angiosperm from which our present day carpel arose.

BIBLIOGRAPHY.

1. Arber, A.: Studies in Floral Morphology, III.
New Phyt., 30, 1931.

2. " : Studies in Floral Morphology, IV.
New Phyt., 31, 1932.

3. " : Floral Anatomy and its Morphological Interpretation.
New Phyt., 32, 1933.

4. Arber, N. and J. Parkin.: The Origin of Angiosperms.
Jour.Lin. Soc. Bot., 38, 1907.

5. Baillon, H.: Natural History of Plants. Vol.I
1871.

6. Balfour, I. Bayley.:Address to the B.A.. 1901.

7. Bancroft, H.: The Arborescent Habit in the Angiosperms.
Ann. Bot., XXIX, 1930.

8. Barratt, K.: A contribution to our Knowledge of the Vascular system of the Genus Equisetum.
Ann. Bot., XXXIV.

9. Behrens, : Untersuchungen über den Anat. Bau des Griffels, und der Narbe.
Gottingen, 1875.

10. Behrens : Die Nectarien der Blüthen.
Flora 1879.

11. Bessey, E. A.: The Comparative Morphology of the Pistils of the Ranunculaceae. Bot. Gaz., 28,189

12. Bessey, C. E.: The Phylogeny and Taxonomy of the Angiosperms. Bot. Gaz., 24, 1897.

13. Bhargava, H.R.: Contribution to the Morphology of Boerhaavia upanda. Jour. Indian Bot. Soc., 11, 1932.

14. Bonnier, G.: Les Nectaires. Ann. Sci. Nat. (Bot.)., VI, 8, 1879.

15. Bower, F.O.: Origin of a Land Flora. 1908.

16. Brongniart, ,: Mémoire sur la Génération et le développment de L'émbryon. Ann. Sci. Nat.(Bot.), ser 1, tome XII, 1827.

17. Brown, R.: On the Relative positions of the Divisions of the Stigma. Misc. Bot. Works of Robert Brown, Roy. Soc., 1866.

18. Bugnon, P.: Organogénèse et Dehiscence de la Gousse des Papillonacées.

19. La theorie du Polymorphism carpellaire et le cas de Légumineuses. Bull. Soc. Bot. France, 72, 1925.

20. Burkill, I.H.: On the Variation of the Flowers o of Ranunculus arvensis.
Jour. Asiatic Soc. Bengal. 71, 1902.

21. Candolle, A. P. de,: Organographie végétale.
Paris. 2 vols. 1827.

22. Capus, M.: Anatomie du Tissue Conducteur.
Ann. Sci. Nat.(Bot.), ser. 6, tome VII, 1897.

23. Cave, M.C.: Structure et Développment du Fruit.
Ann. Sci. Nat. (Bot.), ser. 5, tome X, 1868.

24. Celakovsky, .: Ueber den Phylogenetischen Entwicklungsgang der Blüte. I, II.
Sitzb. de K. Böhm. Ges. Wiss. 3, 1896, and 1900.

25. Chute, H.M.: The Morphology and Anatomy of the Achene.
Amer. Journ. Bot., XVII, 1930.

26. Coulter, J.M.: Contributions to the Life History of Ranunculaceae.
Bot. Gaz., 25, 1898.

27. Coulter and Chamberlain.: The Morphology of the Angiosperms.

27. Eames, A. J.: The vascular Anatomy of the Flower,

with Refutation of the Theory of
Carpel Polymorphism.
Amer. Jour. Bot., XVIII, 1931.

28. Eames, A. J. and Wilson, C.L.: Carpel Morphology in the Cruciferae.
Amer. Jour. Bot., 15, 1928.

29. Eames, A.J. and Wilson, C.L.: Crucifer Carpels.
Amer. Jour. Bot., XVII, 1930.

30. Eames, A.J. and Mac Daniels, L.H.:
Introduction to Plant Anatomy.

31. Eichler, .: Blüthendiagramme Vol.i, 1875.
Vol,ii, 1878.

32. Engler, A.: Beiträge zur Morphologie and Systematik der Ranunculaceae.
Englers Bot. Jahrb., 9, 1888.

33. Engler and Prantl.: Die Natürlichen Pflanzenfamilien. 1888.

34. Goebel, K.: Outlines of Classification and Morphology. 1887.

35. Goebel, K.: Vergleichends Entwicklungs geschichte der Pflanzenorgane.
Schencks Handbuck der Bot., 3, 1894.

Goebel, K.: Organography of Plants. Eng. trans.
Vols. I? and II. 1905.

36. Grégoire, V.: L organogénèse de L'ovaire, et

la Dehiscence du Fruit.
Bull. Soc. Roy. Belgique, 56. 1924.

37. Grégoire, V.: La Valeur Morphologique des Carpels dans les Angiosperms.
Bull. Acad. Roy. Belgique, Cl. Sci. Ser. 5, 17, 1931.

38. Grélot, P.: Recherches sur le Système libéroligneux floral des Gamopétales Bicarpellées.
Ann. Sci. Nat. (Bot.), ser.8, tomeV., 1897.

39. Gueguen, F.: Recherches sur le Tissu collecteur, et conducteur des Phanérogams.
Journ. Bot., 14, 1900.

40. Guéguen, F.: Anatomie comparée du tissu conducteur du style, and du stigmata des Phanérogames.
Journ. Bot., 15,1901, and

41. Journ. Bot., 16, 1902.

42. Guignard, .: Recherches sur le Développment de la Graine, and en particular du tégument séminal.
Journ. Bot, 1893.

43. Harris, T.M.: A New Member of the Caytoniales.
New Phyt., 32, 1933.

44. Hemslow, G.: On the Origin of Floral Aestivation.
Trans. Linn. Soc,, ser. 2, 1880.

45. " : A Contribution to the Study of the Comparitive Anatomy of Flowers.
Proc. Roy. Soc., 1887-88.

46. " : The Origin of Floral Structures.
New York, 1888.

47. " : On the Vascular System of Floral Organs.
Journ. Linn. Soc., 28, 1891.

48. Jackson, G.: Crystal Violet and Erythrosin in Plant Anatomy.
Stain Technol. 1, 1926.

49. " : A Study of the Carpophore of the Umbelliferae.
Amer. Jour. Bot., 20, 1933.

50. Joshi, A.C. and V.S.Rae,: Floral Anatomy of Rivina humilis,L., and the Theory of Carpel Polymorphism.

51. New Phyt., 32, 1933.

51. Klein .: Beiträge zur Anatomie der Inflorescenzahen.
Jahrb. des Bot. Gart. zu Berlin, IV, 1886.

52. Koch, M.F.: Studies in the Anatomy and Morphology of the Composite Flower. I, and II.
Amer. Jour, Bot., 17, 1930.

53. Laborie, .: Recherches sur L amatomie des axes floraux.
Thèse, Toulouse. 1888.

54. Lavaille, P.: Recherches sur le Développment de L'ovaire en Fruit chex les Composées.
Ann. Sci. Nat. (Bot.), ser. 6, tome, XV, 1912.

55. LaCour, L.: Improvements in Everyday Technique In Plant Cytology.

56. Lemaire, A.: De la lignification de quelques membranes épidermiques.
Ann. Sci. Nat. (Bot.), ser. 6, tome XV, 1883.

57. Lestiboudois.: Carpographie anatomique.
Ann. Sci. Nat.(Bot.), ser. 4, tome II, 1854.

58. Lignier, O.: Explication de la Fleur des Fumariacées d'aprés son Anatomie.
C.R. de L Acad des Sc. ,CXXII,1896.

59. Linnaeus .: Prolepsis. 1760.

60. Lonay .: Structure du péricarpe chez les Renonculacées.
Mém. de la Soc. des Sci,, Liege. 1901.

61. Masters, M.: Vegatable Teratology.
Roy. Soc. Pub., 1879.

62. Monnier, Le,: Recherches sur la Nervation de la Graine.
Ann, Sci. Nat., sér. 5, tome XVI.
1892.

63. Mottier, D.M. :Contributions to the Embryology of the Ranunculaceae.
Bot. Gaz., 20, 1895.

64. Oliver and Salisbury,E. J.: Structure and affinity of the Paleozoic Seeds of the Conostoma Group.

65. Orr, M. Y.: The structure of the Ovular Integuments, and the Development of the Testa in Cleome and Isomeris.

66. Parkin, J.: The Evolution of the Infloreseence.
Journ. Linn. Soc., 42, 1914.

67. " : Comments on the Theory of the Solid Carpel, and Carpel Polymorphism.
New Phyt., 25, 1926.

68. Payer, J. B.: Traité d'organogénie comparée de la Fleur. 1857.

69. Rendle, A. B.; The origin of the Perianth in Seed Plants.
New Phyt., 2, 1903.

70. Robertson, C.: The Structure of the Flower, and the Mode of Pollination of the Primitive Angiosperms,
Bot. Gaz., 37, 1904.

71. Sablon, L. de,: Recherches sur la Déhiscence des Fruits à péricarpe sec.
Ann. Sci. Nat.(Bot.), sér. 6, tome XVII, 1884.

72. Sachs, J.: Traité de botanique.

73. Salisbury, E. G.: Variations in Eranthis, etc..
Ann. Bot., XXXIII, 1919.

74. " : On the Morphology and Ecology of Ranunculus parviflorus, L.

75. Saunders, E. R.: A Revisionary Character in the Stock, and the Significance of regard to the Structure and Evolution in the Gynoecium, in the RHoedales, and the Orchidaceae, and other Families.
Ann. Bot., XXXVII, 1923.

76. " : On Carpel Polymorphism. I.
Ann. Bot., XXXIX, 1925.

77. Saunders, E. R.: ON Carpel Polymorphism. II.
Ann. Bot., XLI, 1927.

78. " : On Carpel Polymorphism. III.
Ann. Bot.,

79. " : On Carpel Polymorphism. IV.
Ann. Bot., XLV, 1931.

80. " : On Carpel Polymorphism. V.
Ann. Bot., XLVI, 1932.

81. " : Illustrations of Carpel Polymorphism. I
New Phyt., 27, 1923.

82. " : Illustrations of Carpel Polymorphism. II.
New Phyt.,27, 1923.

83. " : Illustrations of Carpel
Polymorphism. III.

84. " : Illustrations of Carpel
Polymorphism. IV.
New Phyt., 28, 1929.

85. " : Illustrations of Carpel
Polymorphism. V.
New Phyt.

86 " : Illustrations of Carpel
Polymorphism. VI.
New Phyt.

87. Saunders, E.R.: The Inferior Ovary.
New Phyt., 27, 1925.

88. " : On a New View of the Nature of the Median Carpels in the C Cruciferae.
Amer. Journ. Bot., 16, 1929.

89. " : A Reply to Comments on the Thoery of the Solid Carpel, and Carpel Polymorphism.
New Phyt., 25, 1926.

90. " : On some Recent Contributions and Criticisms dealing with Morphology in Angiosperms.
New Phyt., 31, 1932.

91. " : Comments on Floral Anatomy, and its Morphological Interpretation.
New Phyt., 33, 1934.

92. Schnarf, K.: Handbuck der Pflanzenanatomie.
Abt.2, Teil 2, 1929.

93. Schleiden, J? M.: Principles of Scientific Botany. 1849.

94. Sinnott, E.W.: Investigations on the Phylogony of the Angiosperms.
Amer. Journ. Bot., 1, 1914.

Sinnott, E.W.; and Bailey, I. W.?: Investigations on the Phlogeny of the Angiosperms. 3. Nodal Anatomy and the Morphology of the Stipules. Amer. Journ. Bot., 1, 1914.

96. Smith. G. H.: Vascular Anatomy of the Ranalian Flowers. Bot. Gaz., 82, 1924.

97. Tieghem, P. van,: Recherches sur La Symétrie de Structure des Plantes Vasculaires. ANN. Sci. Nat. (Bot.), sér. 5, tome XIII, 1870.

98. " : Note sur les diverse nodes de Nervation de L'ovule et de la Graine. Ann. Sci. Nat. (Bot.), sér. 6, tome VI, 1978.

99. " :Recherches sur la Structure du Pistil, et sur L'anatomie comparée de la Fleur. Mém. Acad. Sci., Paris, 21, 1875.

100. " : Anatomie de la Rose, et en général caractères anatomique des axes invaginés.

Bull. de la Soc. Bot. de France
1878.

101. Teighem, P. van,: Traité de Botanique.
Paris. 1891.

102. Thomas, H. H.: The Early Evolution of the Angiosperms.
Ann. Bot., 45, 1931.

103. " : The Old Morphology and the New.
Proc. Linn. Soc., 145, 17, 1933.

104. " : The Nature and Origin of the Stigma. A Contribution towards a New Morphological Interpretation of the Angiosperm Flower.
New. Phyt., XXXIII, 1934.

105. Thompson, J. M.?: The Theory pf the Leguminous Strobilus.
Pub. Hartley Bot. Lab., 7, 1931.

106. " : The Theory pf the Leguminous Strobilus.
Proc. Linn. Soc., 144, 1932.

107. " : The Theory of Scitaminean Flowering.
Pub. Hartley Lab., 11, 1933.

108. " : Comments on Recent Statements regarding the Nature and

Origin of the Angiospermic Stigma.
New Phyt., XXXIII. 1934.

109. Thompson, J. M.: Studies in Advancing Sterility. The State of Flowering known as Angiospermy.
Pub. Hartley Lab. Bot., 12, 1934.

110. Trécul, .: Observations sur Les Fruits des Prismatocarpus.
Ann. Sci. Nat., sér. 6. tome XX, 1843.

111. " : Recherches sur L'ordre d apparition des Premiere Vaisseaux dans les Organs aériens.

112. Troll, W.: Morphologie der Schildformigen Blätter.
Planta, Teil II, 1932.

113. Velenovosky, J.: Vergleichende Morphologie der Pflanzen.
Teil III, 1910.

114. Vesque, .: Développment du Sac embryonnaire des Angiosperms.
Ann. Sci. Nat.(Bot.)? sér. 6, tome VI, 1878.

115. Vuillemin, P.: Les Anomialies Végétables.
Paris. 1926.

116. Warming, M.E.: De L'ovule.
Ann. Sci. Nat.(Bot.), sér, 5,
tome VI, 1878.

117. Warming and Potter, Systematic Botany.

118. Wernham, H.F.: Floral Evolution with particular
Reference to the Sympetalous
Dicotyledons.
New. Phyt., X, 1911, and

119. " New Phyt., XI, 1912.

120. Wollf, K. F.: Theoria Generationis. 1759.

121. Worsdell, W. C.: The Principles of Plant
Teratology. Vol. II.
London. 1916.

122. " : The Origin of the Perianth
of Flowers.
New Phty., 2, 1903.

123. " : The Structure and Morphology
of the Ovule: an Historical
Sketch.

124. Yen, T. K.: Observations on the Sex Differentiation, and the Flower Anatomy of
Firma simplex.

Sci. Soc. of Chona, Nanking, 1929.

125. Yen, T. K.: Carpel Dehiscence in Firmiana simplex.
Bot. Gaz., 93, 1932.

126. Goethe .: Metamorphises of Plants.
English Trans..
Seemann's Journ. Bot., 1863.

DESCRIPTION OF FIGURES.

Trollius - Garden Variety.

Figs. 1 - 2. From transverse serial sections taken at successively higher levels. (x 30).

Fig. 1, A. Transverse section of the flower stalk. Nine ridges occur with the corresponding number of large vascular bundles. In the furrows there are varying numbers of smaller bundles. Three sepals are in the plane of section.

B. At the level of insertion of the sepal bases the ridges disappear. The bundles in the sepal bases are fusing with one another.

C. Three of the perianth segments are in the plane of the section. There are five bundles from each segment entering the cortex.

D. The supply from segments 1, 2, and3, is appraochong that of the main ring of bundles. The vascular supply of nine segments may now be seen.

Fig. 1, A. The bundles from the first three

segments are now entering the main stele.

B. The Supply from segments, 4,5,6,7,8, and 9, are passing in through the cortex, three bundles from each segment, excepting segments 4 and 5.

C. Segment 10 is now in the plane of section.

D. The traces from the segments have entered the main ring of bundles, and traces to the honey leaves have now been given off and are passing out through the cortex.

Fig. 3, A. Transverse section of another flower stalk, showing the variation in the number of bundles present. (x 18).

B. Transverse section through the receptacle, at the level of formation of the carpellary traces, showing stamen traces passing out through the cortex on the one side, and carpels on the other - above the level of formation of the laculus. (x 30.).

Fig. 4, A -G. From transverse serial sections taken at successuvely higher levels, at the level of formation of the carpellary traces. Only a small portion of the receptacle is shown.

Diagram III is a reconstruction of this series. The numbers of the bundles correspond in the two drawings. (x 30).

Fig. 5, A - D. Macerated preparations of carpels. For details see text. (x 10).

Fig. 6, A - E. Detailed drawings of the marginal and midrib bundles.

A. The midrib bundle.

D. The marginal bundle at the same level as A. (x 500).

B. A low power drawing to show the level at which A and D were drawn. (x 62).

E. At a higher level the midrib has divided, and the two branches are seen - one on either side. (x 500).

C. A low power drawing of E. (x 62).

Fig. 7, A - B. Transverse serial sections at successively higher levels in the style. (x 500).

A. The midrib only consists of two two vessels, while the marginals are well developed.

B. Only the marginal bundles remain.

Note the conducting tissue at the apex of the style.

CALTHA PALUSTRIS.

Fig. 8, A - F. To illustrate the variation in the perianth supply. (x 30).

A. Three gaps are formed by the departure of the traces to a segment. Two bundles lie between two gaps in the one case, one in the other.

B. Three gaps are formed. One bundle lies between each gap.

C. and D. Several gaps are formed. Numerous traces enter the base of the segment, and the midrib branches on its passage through the cortex.

E. A single gap is formed by the departure of the traces.

F. Two gaps are formed separated by a single bundle.

Fig. 9, A - B. Transverse serial sections at successively higher levels. (x 18).

A. At the level of formation of the carpellary traces.

B. The midrib bundles have entered the carpellary base and the marginal bundles are being formed.
These drawings represent in transverse section Diagram IV.

C. Transverse section through the receptacle at the level of formation of the carpels. The carpel X is supplied by the division of a single bundle, excepting the fusion of one of the bundles left after the departure of midrib trace, with a small receptacular bundle. (x 18).

Fig. 10, and fig. 11. Transverse serial sections through the receptacle at successively higher levels.

A. Illustrates the division of the receptacular bundles to supply the midirbs of the carpels. (x 18.).

B. Shows the behaviour of the bundles after the departure of the midrib traces. (x 18.).

Fig. 11, The pith is traversed by numerous bands of phloem. At the base of some of the carpels the marginal bundles are dividing so as to form two equal bundles. (x 30.).
Diagram V is a reconstruction of this series.

Fig. 12, A - C. Transverse serial sections at successively higher levels above the level of departure of the stamen traces. (x 18.).

A. Illustrated the position and size of the receptacular bundles, at the level of departure of the last few stamen traces.

B. A few traces which will become the midribs of the corresponding carpellary traces are passing out through the cortex.

Fig. 12, C. In this figure the small strands left by the midrib bundle, on its passage through the cortex can be seen within the carpellary base. This series corresponds to Diagram VI.

Fig. 13, A - C. A series of sections illustrating the fourth type of division of the receptacular bundles which form the carpellary supply. (x 18.).

A. The last stamen traces are passing out through the cortex.

B. The traces which will supply the carpellary midrib are being formed.

C. At the base of the loculus one or two bundles may be present. Bundles 7, amd 3 are dividing to give rise to a midrib trace to a carpel.

Fig. 14. A. The midrib bundle of a carpel. (x 500.).

B. The corresponding marginal bundle. (x 500.).

Fig. 15, A - G. Whole and half carpels mounted to show the secondary venation of the carpellary wall, with special reference to the branches from the midrib bundle, and the stylar supply. For details see the text. (x 10.).

Fig. 16, A - B. A longitudinal section through a carpel showing the branching of midrib bundle.

A. A low power drawing, showing three branches passing out round the wall. (x 18.).

B. One lateral under high power. (x 500).

Fig. 17. A - C. The stylar supply.

A. The midrib and marginal bundles have fused to form an arc of vessels surrounding the stylar canal. The outer epidermal cells of the canal have become broken down, and the subepidermal layer of cells now form the outer epidermis. (x 500).

B. The mdirib bundle has divided in

the style. (x 500).

C. The style drawn under low power, showing the two branches given off by the midrib, and the marginal bundles, which end blindly in that position.

HELLEBORUS ORIENTALIS.

Fig. 18, fig. 19, and 20. Illustrate the method of departure of the perianth traces, and the mode of branching of the remaining stelar bundles, up to the level of the traces to the honey leaves. In the tangentially elongated bundles the phloem has stippled, so that the position of the xylem vessels may be seen. (x 30).

Fig. 18, A. A transverse section of the flower stalk ; the radially elongated bundles form the vascular supply to the perianth segments, and the tangentially elongated bundles give riseto the supply to the remaining whorls.

B. One of the radially elongated bundles has divided into three, while still within the ring of of vascular bundles.

C. One of the perianth traces is Passing out through the cortex, and two bundles have divided into three within the main stele. Of the tangentially elongated bundles, two have become deeply concave, whilst a third has become tangentially expanded, which is the first stage in the formation of the concentric bundle. From bundle 1, a small portion has been detached on the one side.

D. The remaining two bundles which will supply the perianth segments have divided into two within the main ring of tissue. Bundle 1 has now become concentric, and some of the vessels have continued to pass outwards, and are deeply concave The small strand still persists independently. Bundle 2 has now

divided and given rise to two strands, with the xylem vessels deeply concave. Bundles 3, and 4 are becoming concave.

Fig. 19. A. The marginal bundles of three of the perianth traces are passing out through the cortex. In two cases a marginal strand is passing out previous to the division of the remaining portion of the corresponding bundle. In bundle 1 the small strand has become part of the bundle in which the xylem is deeply concave. This bundle has passed further out into the cortex. From bundle 2 two concentric bundles have been formed, and from each a portion has been detached. Bundle 3 is now deeply concave and a small portion is going to be detached at a higher level from the one side. Bundles 4, and 5 are becoming deeply concave.

B. The perianth traces are passing out

through the cortex. Two concentric bundles have been formed from bundles 1 and 4, one bundle in each case lying further out in the cortex. In bundle 3, as the original strand became concave a small portion was detached on the one side, and later a similar portion on the other side. These are lying furthest removed from the main bundle. As the main bundle became concentric, two parts were detached, and these eventually formed the central bundle, also at this level, concentric. A small strand has been detached from bundle 5, and the main bundle is becoming concentric.

C. Seven traces can be seen entering the base of one of the perianth segments. Division has occurred as the bundles passed through the cortex. In bundle 1, the second concentric bundle is commencing to divide into two. The xylem at the

point nearest to the first formed circle, passes outwards. The whole bundle becomes tangentially expanded and finally, with the continued outward passage of the xylem vessels, two concentric bundles are formed. Bundle 5 has divided into concentric bundles, a small strand has been split off by each.

D. The marginal bundles are entering three of the perianth segments, previous to the inward passage of the midrib. In bundle 1, the vessels from one of the newly formed circles has passed back and fused with the parent bundle. The other concentric bundle is approaching the main axial cylinder. Bundle 3 has become further subdivided. One of the small strands has become concentric, and split off a small portion. The large concentric bundle has passed bach towards the main ring and given off a small portion.

Fig. 20. A. The second concentric circle is now lying in the main ring of bundles, in the case of bundle 1. There are now formed from bundle 2 two bundles in the main ring of tissue, and a small strand left in the cortex. The cortical bundles in the remaining strands are passing back towards the main ring.

B. In bundle 1 there is a strand in the cortex and one of the two main bundles is dividing into three. One of the strands in bundle 2 has split off a potion which is passing out through the cortex. The central strand of the three smaller bundles in bundle 3 is passing outwards, while the other two are passing in towards the main axis. In bundles 4 and 5 there are two concave bundles and two smaller strands.

C. The two main portions is bundle 2 are dividing into three parts. In bundle 3, two strands are fusing with the

main divisions of the parent bundle. In bundles 4. and 5 two main axial strands result from the divisions of the bundles, and a portion remains out in the cortex.

D. The traces to the two last formed perianth segments are entering the base of each segment. The first three perianth gaps have been closed. Bundles 1 and 2 have divided, while in bundles 3, 4, 5, there are two main axial bundles, and the perianth gpas have not been closed by the expansion of the former. The traces to the first formed nectaries are passing out through the cortex.

Fig. 21, A - D. The figures illustrate the method by which bundle 1 becomes concave, and the splitting off of two portions. (x 500).

Fig. 22, and fig. 23. Trasnverse serial sections sections taken at successively higher levels, to show the formation of the carpellary traces, and their position

within the carpel base. Reconstruction of the course of the bundles is shown in in Diagram VIII. For details see the text. (x 30).

Fig. 24, A. The midrib bundle and the two flanking strands, which are lateral branches from the marginal bundles. (x 400).

B. The marginal bundle at a corresponding level. (x 400).

C. The level of the carpel at which A, and B were drawn. (x 18).

D. The marginal bundle at the level of insertion of the last ovule. (x 400.).

Fig. 25, A. At the base of the style, the marginal bundles reappear and there is an increase in the number of vessels. The midrib with the two lateral branches from the marginal bundles is also seen. (x 400)

B. The marginal bundles have fused with lateral branches, and form vessels surrounding the stylar canal. (x 400).

C. At the apex of the style there is a single strand - the marginals having fused with the midrib. (x 500).

D. A stoma present on the inner wall of the carpel. (x 300).

Fig. 26, A to C. Illustrations of the venation of the carpellary wall. (x10).

HELLEBORUS FOETIDUS.

Fig. 27, A to C. The secondary venation in the carpellary wall. (x 10.).

Fig. 28, A to C. Transverse serial sections at successively higher levels, showing the vascular supply to the perianth segments and the mode of branching of the remaining bundles. (x 30).

A. Transverse section of the peduncel showing two perianth traces leaving the main ring of tissue. The tangentially elongated bundles have commenced to divide, after having elongated tangentially.

B. Three of the perianth traces are passing out through the cortex. One of the traces has divided into three in the cortex. All of the tangentially elongated bundles, excepting one, have divided into varying numbers of small strands, each of which

has divided into a concentric bundle. One of the bundles has given off a small trace.

C. The perianth traces are passing out through the cortex, and the marginal bundles are dividing. The concentric structure of the main stelar bundles is broken down. The vessels are running obliquely round the receptacle. Due to this expansion the gaps are becoming closed.

Fig. 29, A - F. Transverse serial sections at successively higher levels showing the origin and behaviour of the carpellary traces. (x 30).

A. Three stamen traces are passing out through the cortex, and one of the gaps is closed. The two midrib traces to the carpel, M, are are still within the main ring of bundles.

B. One of the stamen gaps is not closed. A small group of vessels have become detached from the main bundle, and have come to lie on one side of the midrib bundle.

C. The two carpellary midribs are passing out through the cortex. The stamen gaps are all closed.

D. The main groups of xylem vessels are moving

apart.

Fig. 29, E. Two gaps are formed. One of the small groups of vessels is passing out round the loculus. In the other caprel, a strand passes out towards the midrib, but ends blindly.

F. At the base of each carpel there are two marginal bundles. Laterals may be seen in the carpellary wall.

Fig. 30, A. Transverse section through the receptacle, in a flower possessing three carpels. Two of the stamen gaps are closed. (x 30).

B. The margins of the carpels have become delimited , previous to the disappearance of the connecting parenchyma. (x 30).

C. Transverse section through the receptacle of a flower in which there is no cell division in the pith. Two midrib bundles can be seen leaving the stele.

D. The bundles between the two strands M, divide to form the marginal supply to one margin of two adjacent carpels.

Fig. 3i, A. The lateral branches from the marginal

bundles are fusing with the midrib in the style. (x 500).

Fig. 31, B. A low power drawing, showing the arrangement of the bundles in the style. (x 108).

C. A "nest" of meristematic cells in the pith. (x 500).

D., E., F., Illustrate the development of the hairs. (x 500).

HELLEBORUS VIRIDIS.

Fig. 32, A. Transverse section of the flower stalk The xylem has died out in the tangentially elongated bundles. (x 30).

B. At a higher the level the vessels reappear, but as small individual strands (x 30).

C. A transverse section of the peduncel. (x 30).

D. The radially elongated bundles contain numerous vessels, which persist.

E. The perianth supply is passing out. The heavily lignified tangentially expanded bundles have elongated, and

become divided into numerous strands.

E. (x 30).

F., and G., The tangentially elongated bundles continue to become divided up into numerous smaller strands, and close the perianth gaps. (x 30).

Fig. 33, A - B. Transverse serial sections through the receptacle at successively higher levels, showing the formation of the carpellary traces. For details see the text. This corresponds to diagram XII. (x 30).

ERANTHIS CILICICA.

Fig. 34 A - D. Transverse serial section through the receptacle at successively higher levels, showing the supply to the bracts and the perianth. (x 30).

A. The peduncel.

B. Six bundles form the supply to the bracts.

C. Seven bundles divide to supply the bracts.

D. Traces are passing out to supply the perianth segments. Note the division of the midrib bundle.

Fig. 35, A - D. Transverse sections at successively higher levels to show the origin of the carpellary traces. For details see the text. Diargam Xiv represents the bundles in longitudinal section. (x 30).

Fig. 36, A - C. A similar series to show the variation which occurs when there are a greater number of carpels developed. See diagram XV and the text. (x 30).

Fig. 37, A., and B. The midrib and marginal bundles in the pedicel. (x 300).

C. A low power drawing to show the arrangement of the bundles in the pedicel. (x 30).

D. The midrib bundle in the style. (x 500).

E. An epidermal hair. (x 500).

ERANTHIS HYEMALIS.

Fig. 38, A-C. Transverse serial sections at successively higher levels, to show the origin of the carpellary traces. This represents in transverse series diagram XVI. (x 30).

Fig. 39, A - B. Eranthis cilicica. The venation of the carpellary wall. (x 10).

Fig. 40, A - B. Eranthis hyemalis. The venation of the carpellary wall. (x 10).

CIMICIFUGA DAVURICA.

Fig. 41, A - C. The peduncel and perianth supply.

A. The type where sclerenchyma is present forming two arcs of tissue. (x 108).

B. A complete ring of sclerenchyma surrounds the bundles. (x 108).

C. The supply to the perianth segments. A single bundle passes out through the cortex, and divides into three within the base of the segment. (x 108).

Fig. 42, A - F. The carpellary supply. (x 108).

A. Five carpels are developed, two near the centre of the receptacle.

B. Six carpels are formed.

C. Two bundles pass into the centre of the receptacle and fuse. At a higher level this bundle enters a pedicel.

D - F. A series at successively higher

levels illustrating a type of division of the receptacular bundles.

Fig. 43, A. The bundles in the style. The marginals are fusing with the midrib. (x 500).

B. and C. Cimicifuga racemosa.

B. The midrib bundle at the base of the carpel. (x 500).

C. The midrib bundle in the style, showing the increased lignification. (x 400).

Fig. 44, A - C. The secondary venation in the carpellary wall.

CIMICIFUGA RACEMOSA.

Fig. 45, A - C. Transverse serial sections illusrtating the perianth supply, and the division of the stele into numerous strands by the departure of the stamen traces. (x 108).

Fig. 46, A - C. The apex of the receptacle near the level of formation of the carpellary traces, up to the base of the carpel. For details see the text.

Fig. 47, A- C. Transverse serial sections at success-

ively higher levels. Division of the midrib bundle occurs, prior to its outward passage, and also branches as it runs out through the base of the carpel. The course of the branches are seen in figs. B and C. (x 108).

Fig. 48, A - C. The secondary venation in the carpel wall. Note the branches from the midrib in A and C. (x 10).

Fig. 49, A. The bundles in the peduncel. (x 108).

B. A bundle dividing to supply a perianth segment. (x 108).

C. The bundles in the pedicel form a solid ring of vascular tissue, and this is broken by the supply passing out to a perianth segment. (x 108).

Fig. 50. A - C. Transverse serial sections to show the origin of the carpellary traces, and a single strand entering the base of each carpel. A and B x108. C x 62.

Fig. 51. A single carpel of Xanthorhiza.

N.B. The magnification given is that of the original drawing. All have been reduced on being photographed.

In the diagrams, the midrib is represented by a heavier line. This does not necessarily mean that the midrib is the more heavily ligmified bundle.

TROLLIUS- GARDEN VARIETY.

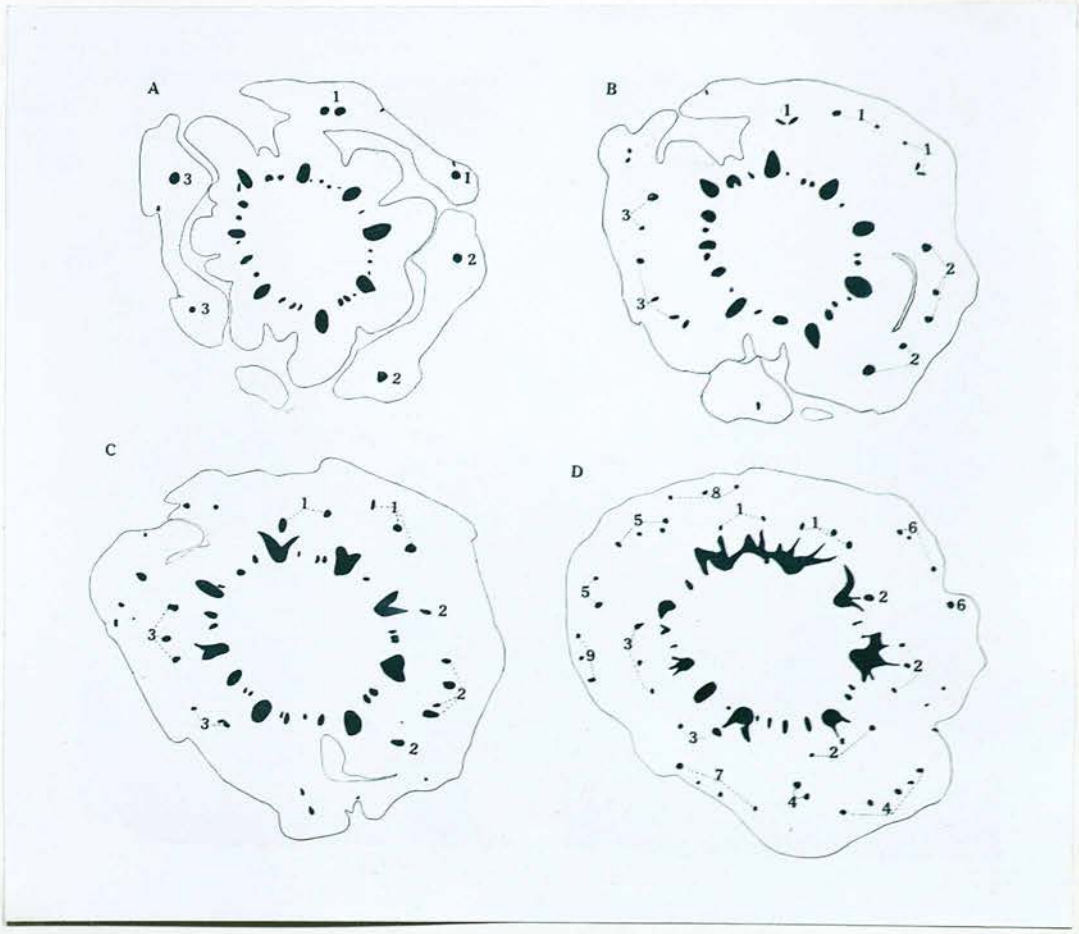


Fig. 1.

TROLLIUS - GARDEN VARIETY.

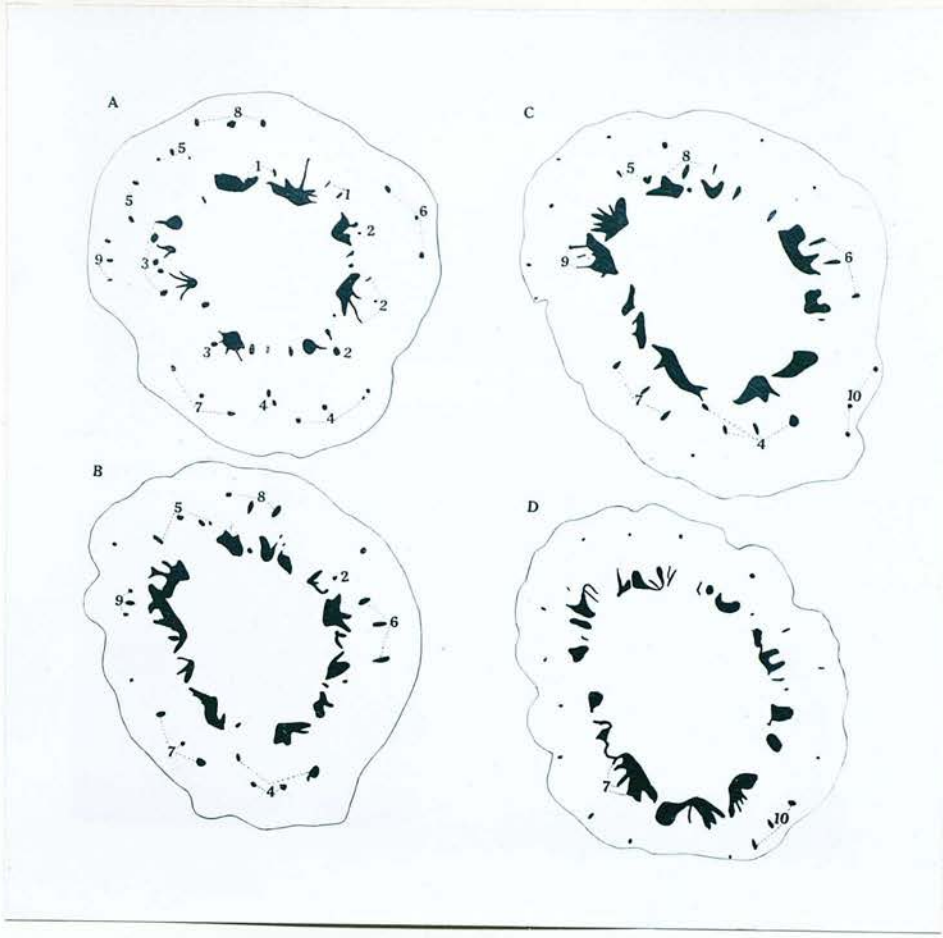


Fig. 2.

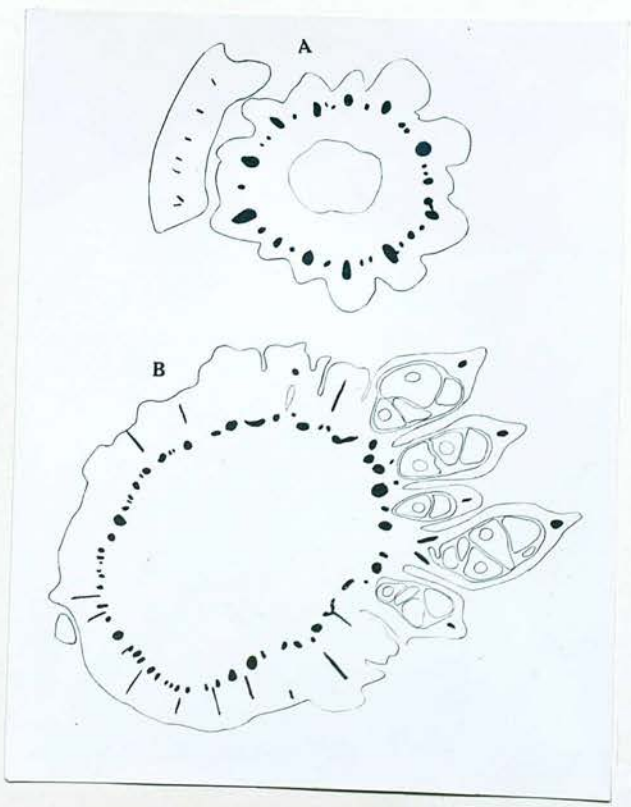


Fig. 3.

TROLLIUS - GARDEN VARIETY.

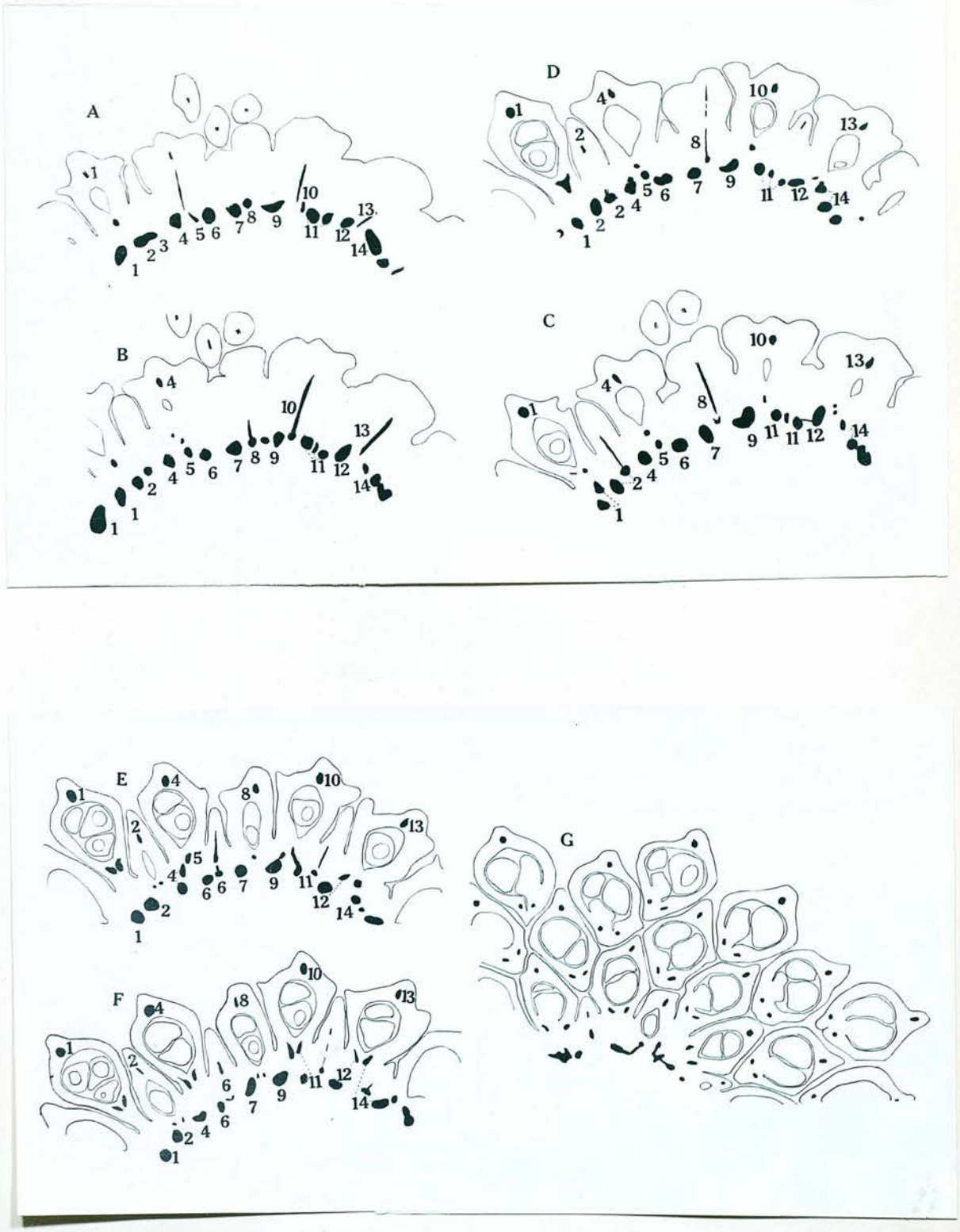


Fig. 4.

TROLLIUS - GARDEN VARIETY.

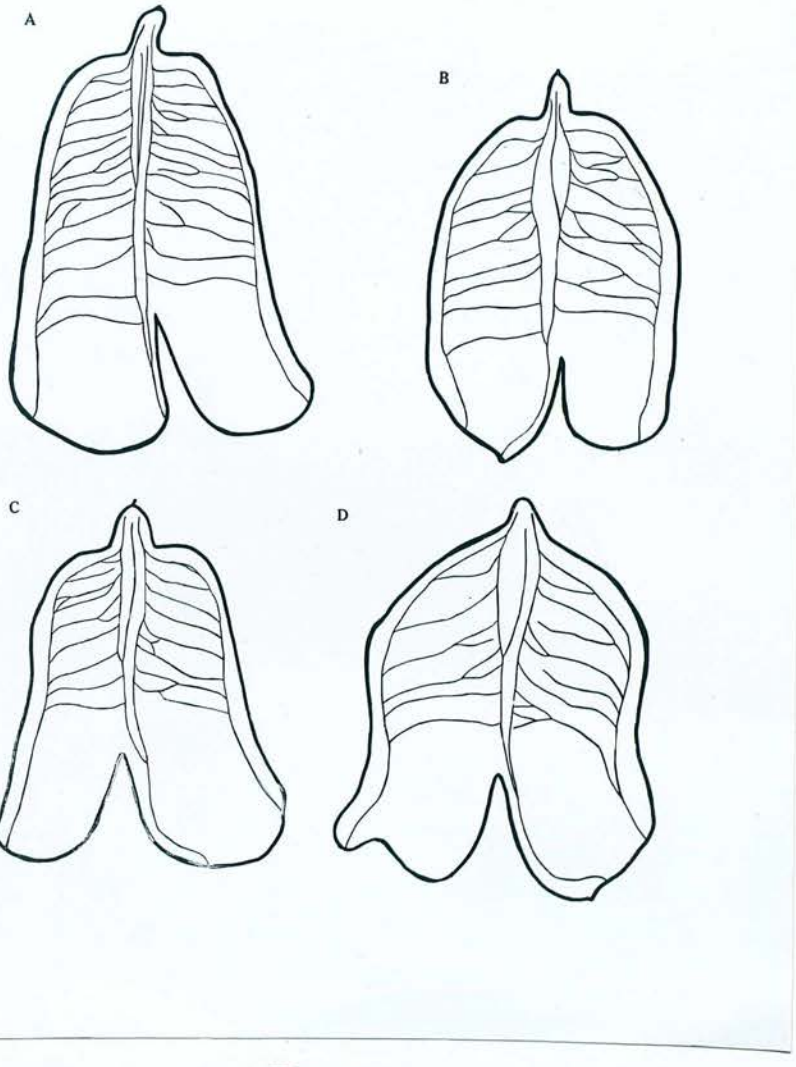


Fig. 5.

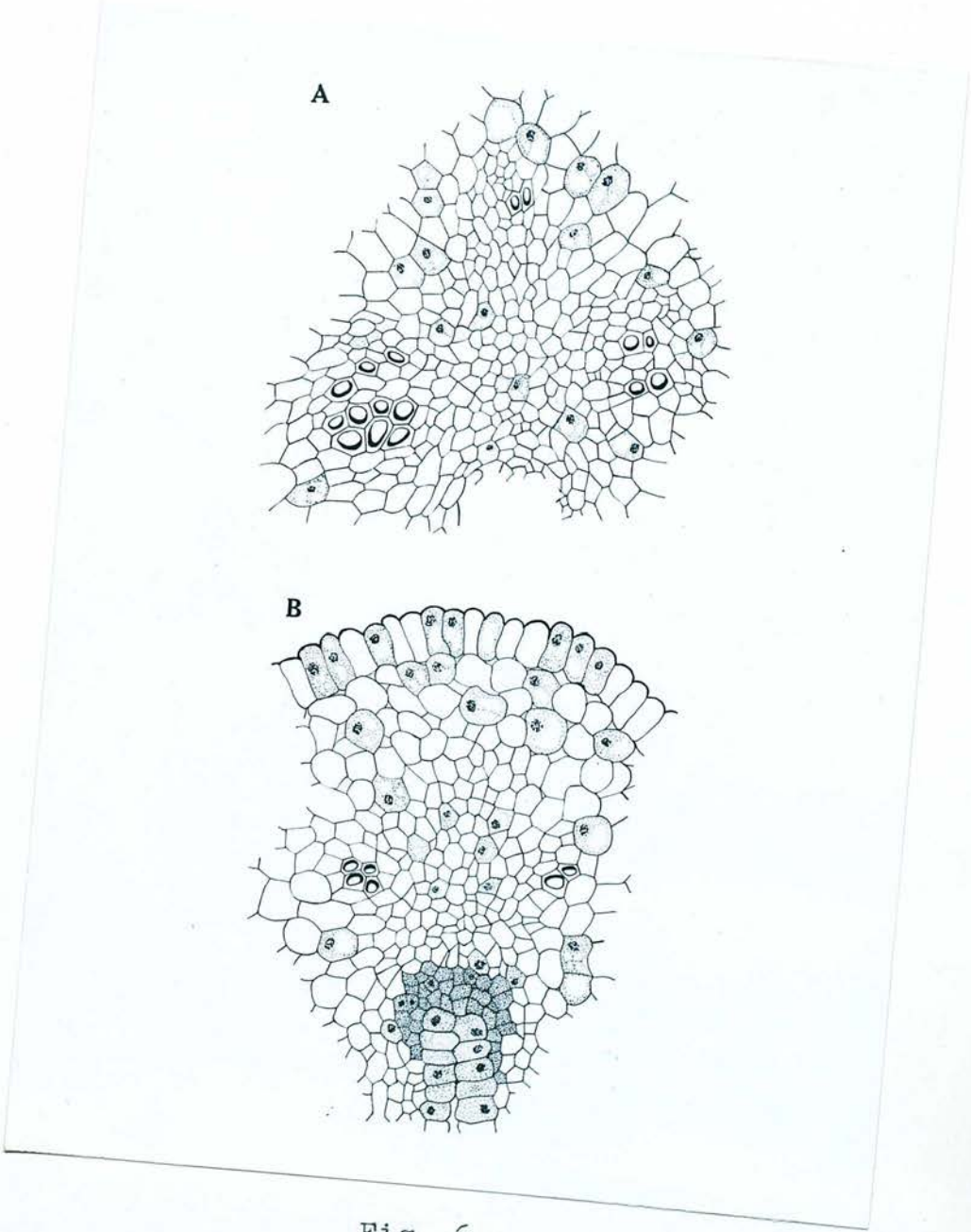


Fig. 6.

TROLLIUS - GARDEN VARIETY.

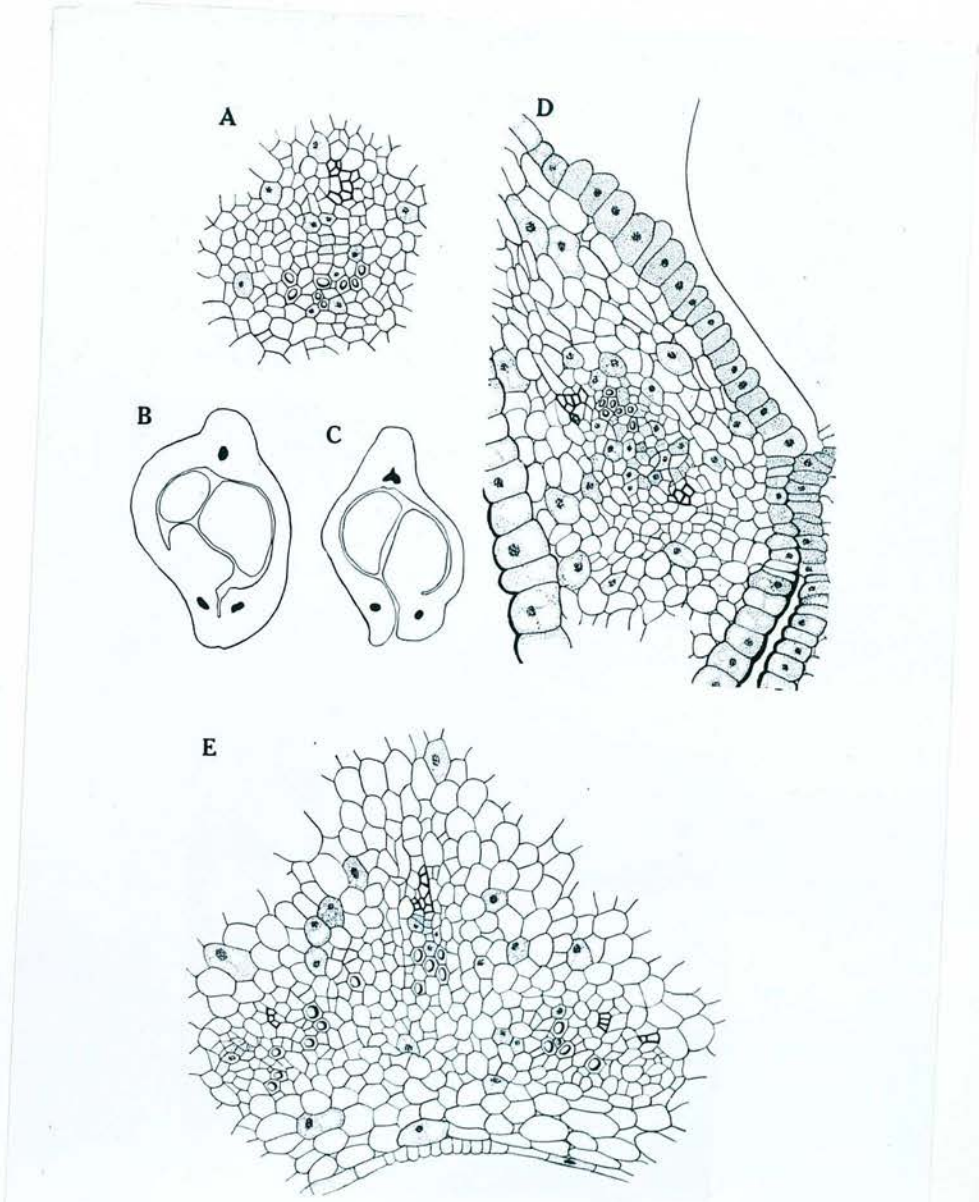


Fig. 7.

CALTHA PALUSTRIS.

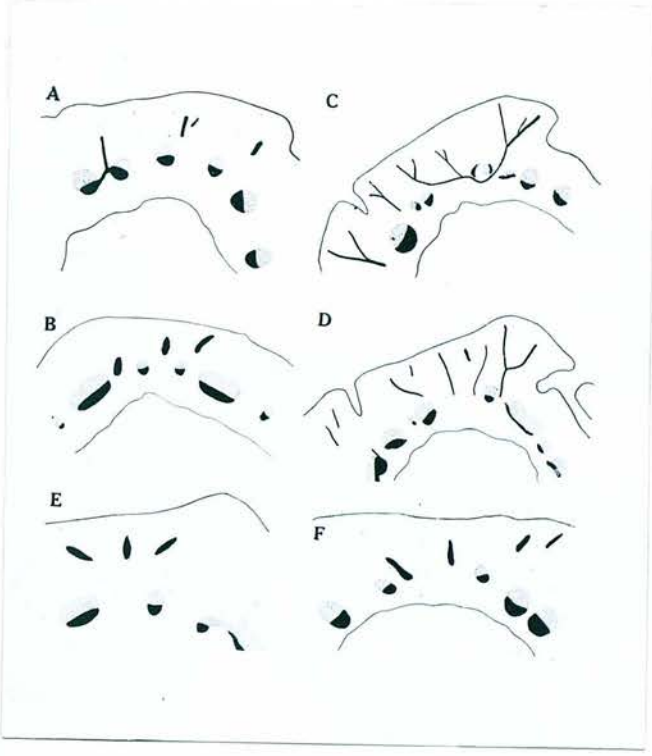


Fig. 8.

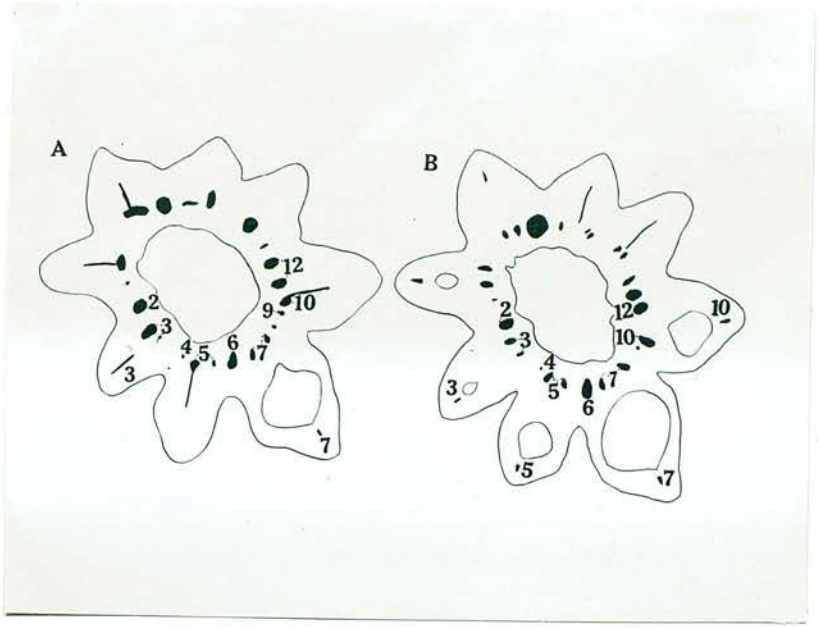


Fig. 9.

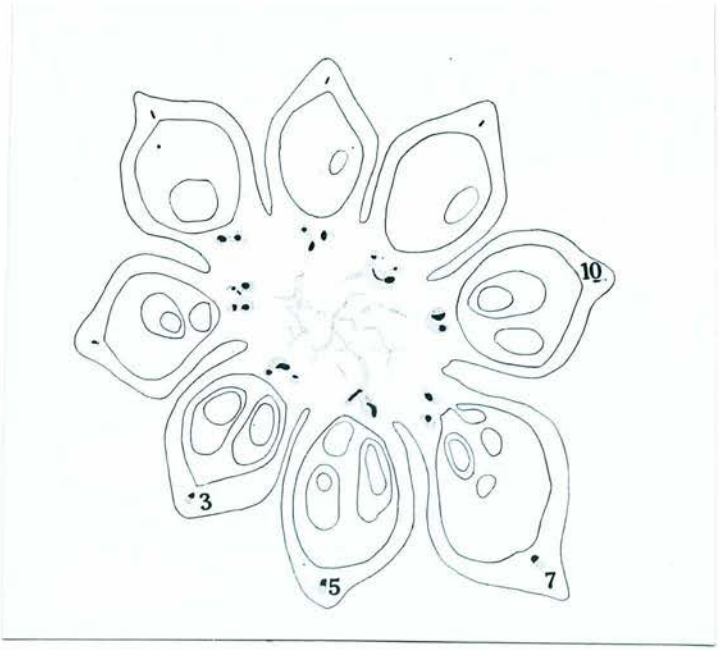


Fig. 10.

CALTHA PALUSTRIS.

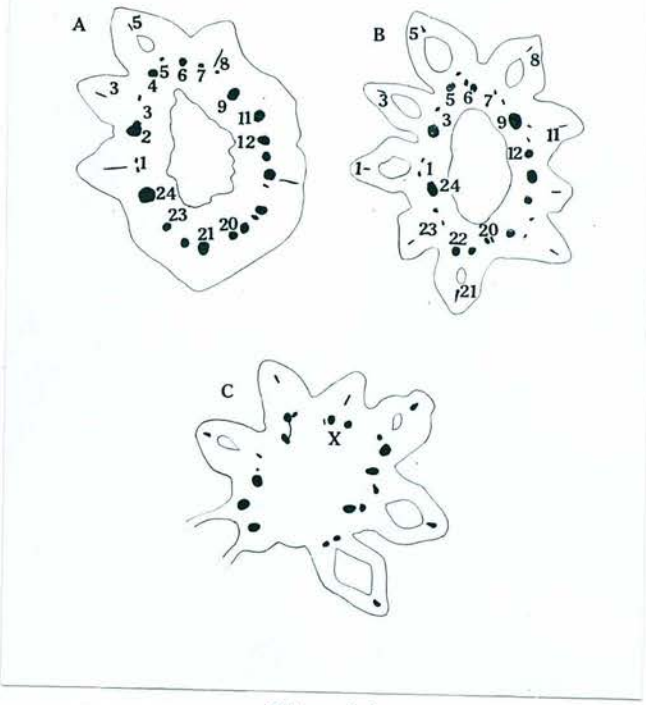


Fig. 11.

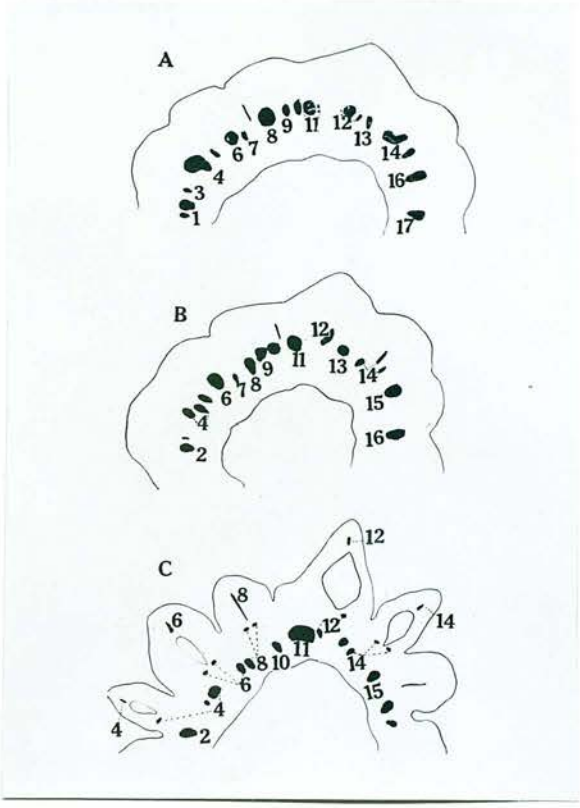

A
1 2 3 4 6 7 8 9 11 12 13 14 16 17
B
2 4 6 7 8 9 11 12 13 14 15 16
C
2 4 4 6 8 10 11 12 12 14 14 15 6

Fig. 12.

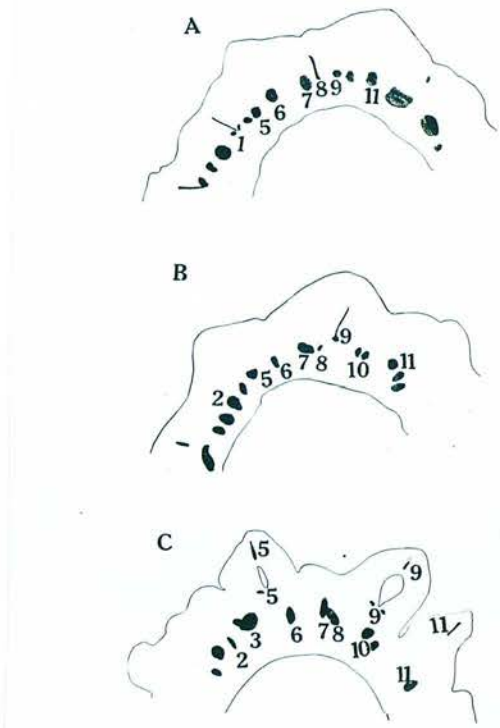

A
1 5 6 7 8 9 11
B
2 5 6 7 8 9 10 11
C
2 3 5 5 6 7 8 9 9 10 11 11

Fig. 13.

CALTHA PALUSTRIS.

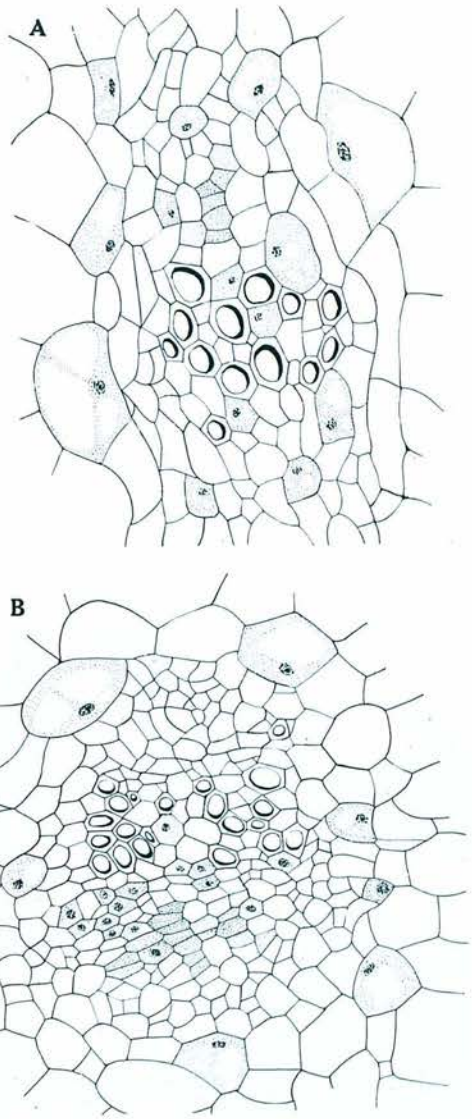
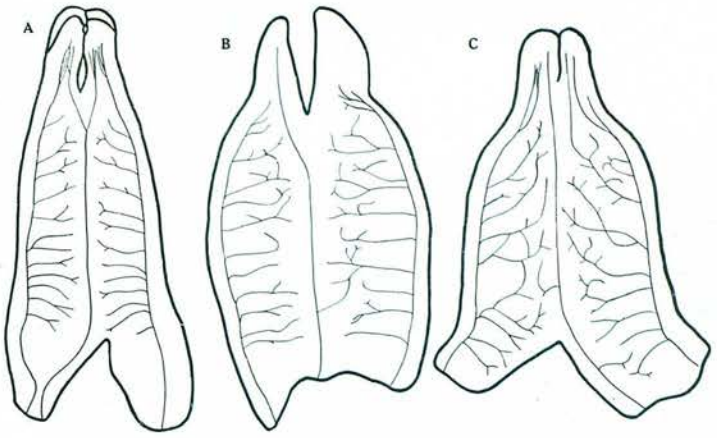
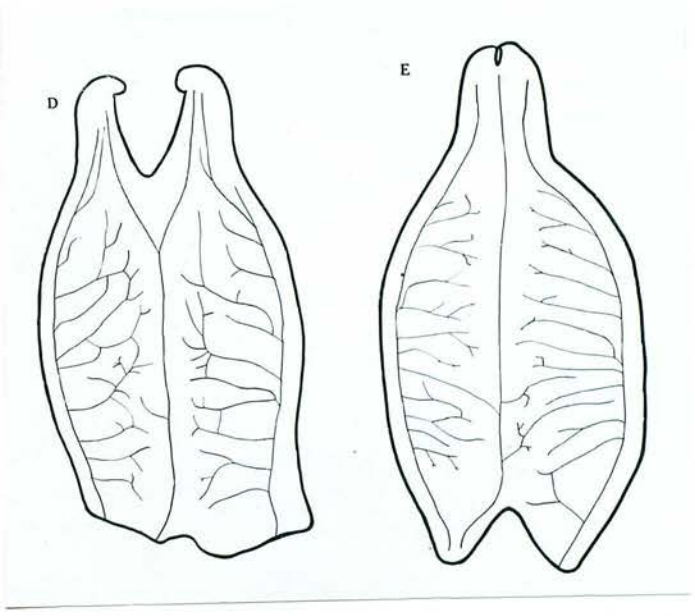


Fig. 14.





CALTHA

PALUSTRIS.

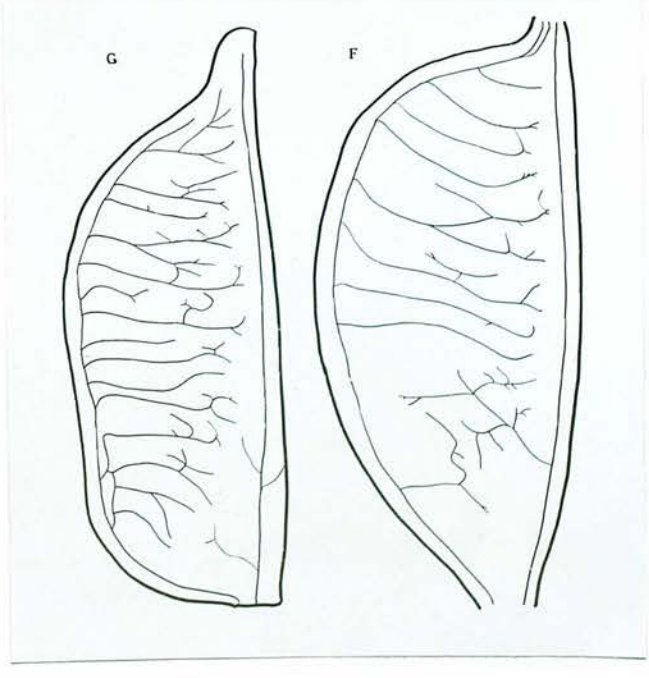


Fig. 15.

CALTHA PALUSTRIS.

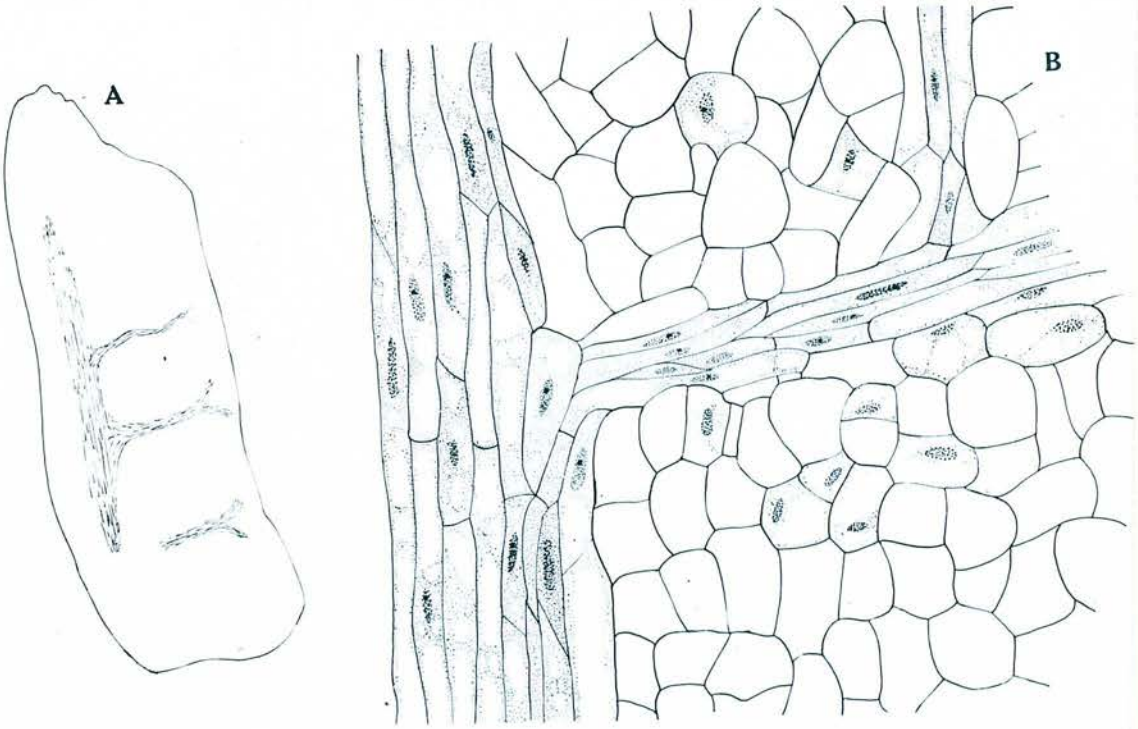


Fig. 16.

CALTHA PALUSTRIS.

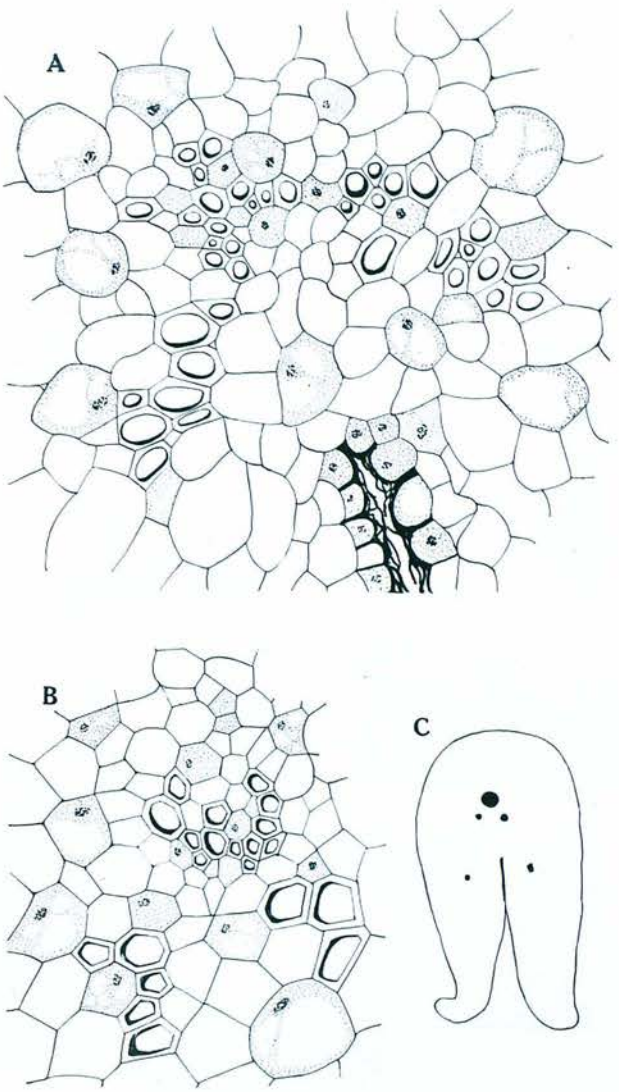


Fig. 17.

HELLEBORUS ORIENTALIS:

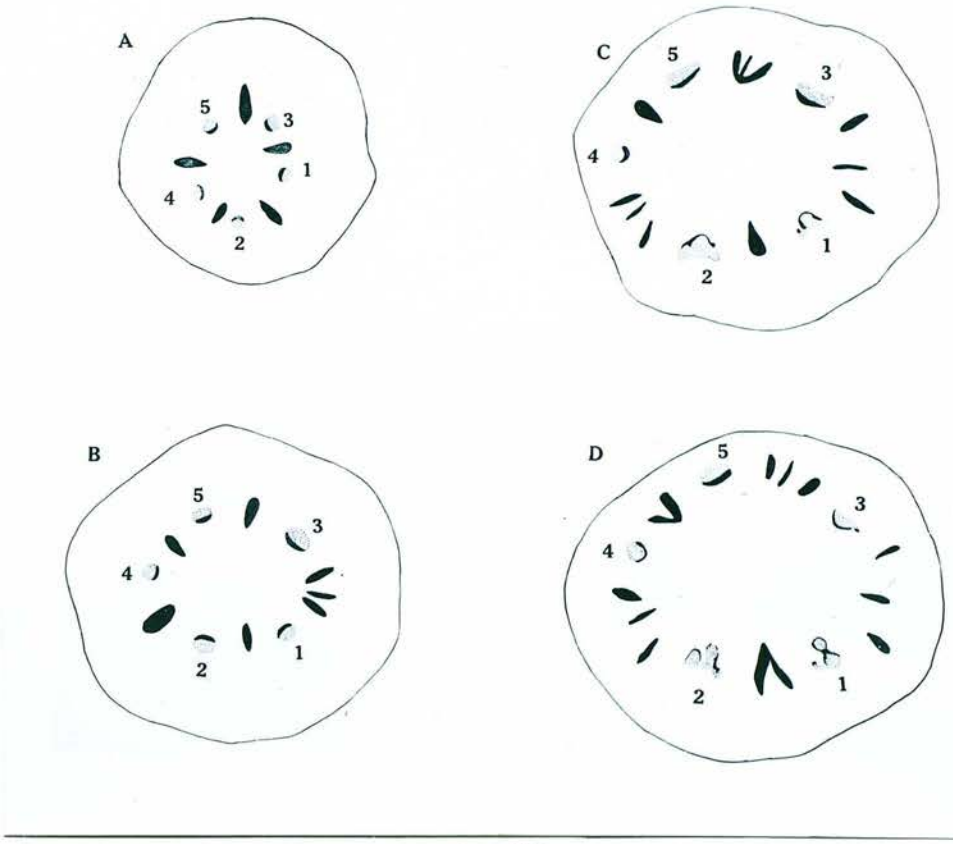


Fig. 18.

HELLEBORUS ORIENTALIS.

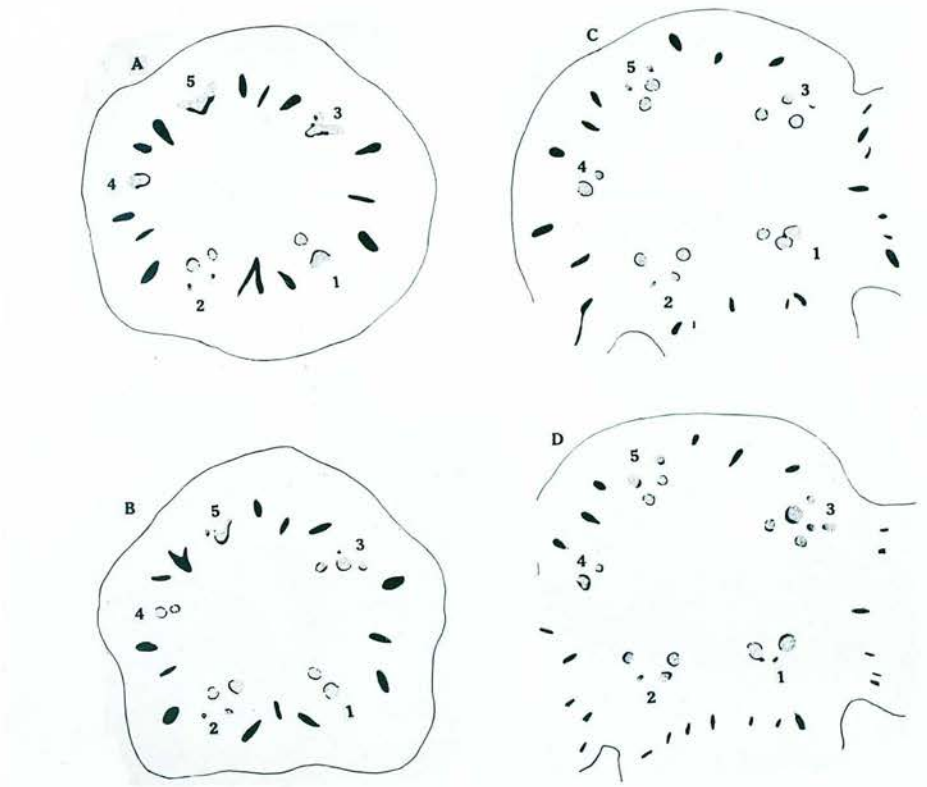


Fig. 19.

HELLEBORUS ORIENTALIS

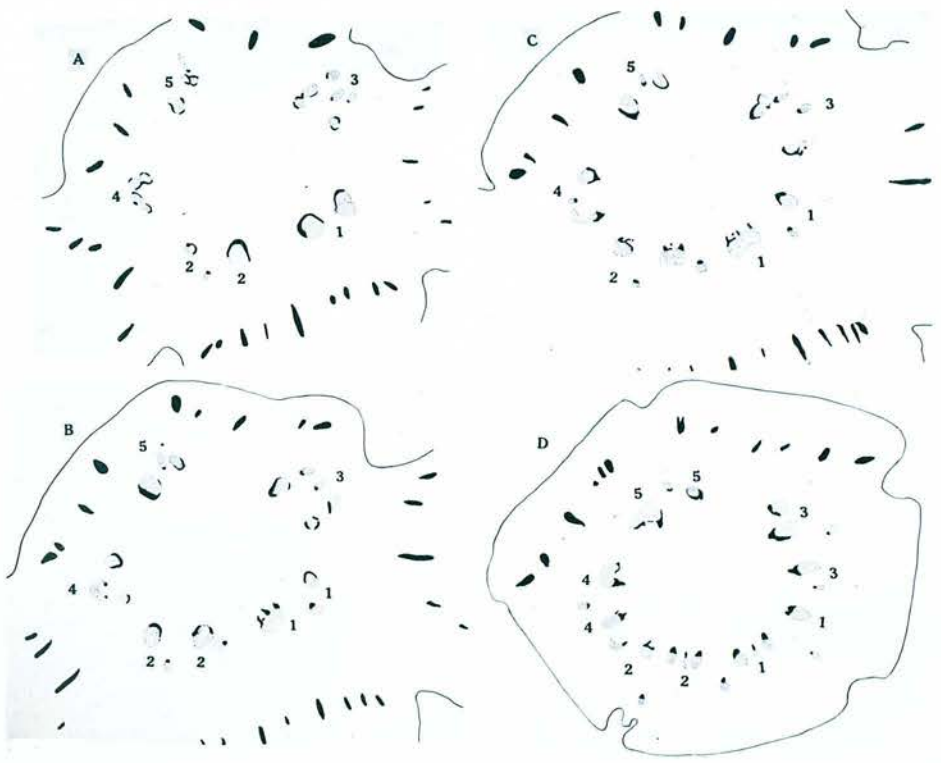


Fig. 20.

HELLEBORUS ORIENTALIS.

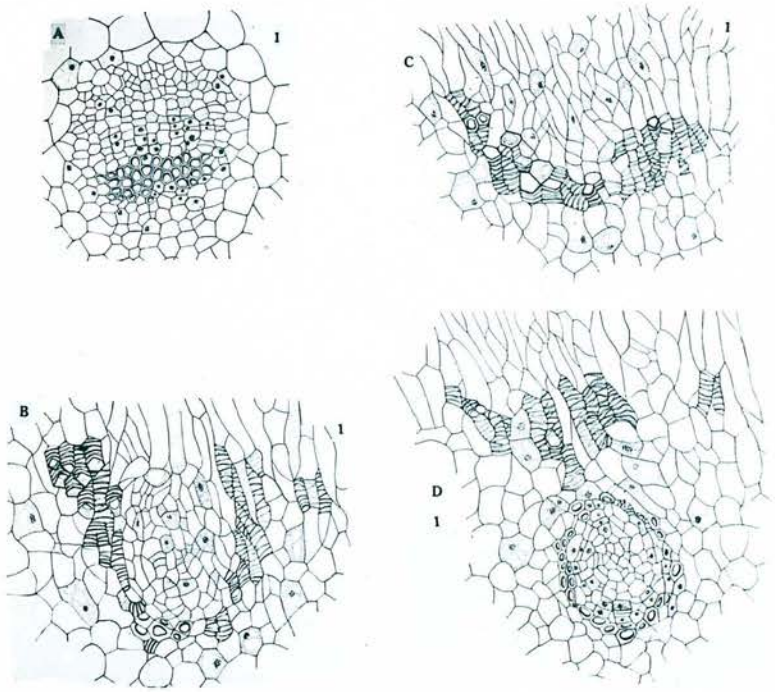


Fig. 21.

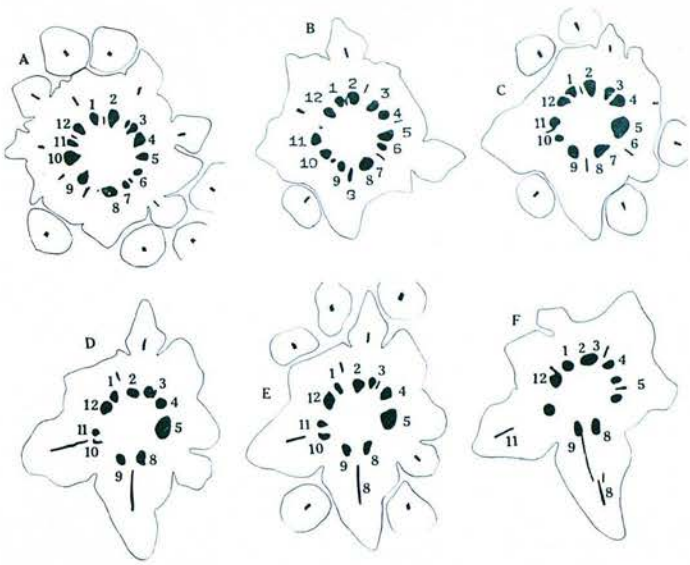


Fig. 22.

Fig. 23.

HELLEBORUS ORIENTALIS.

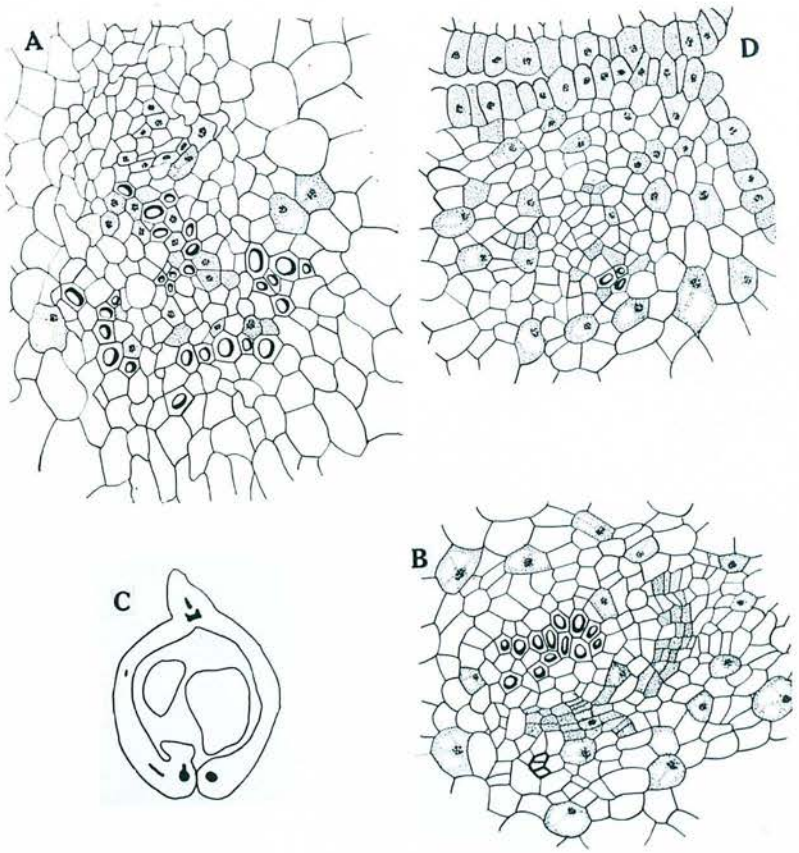


Fig. 24.

HELLEBORUS ORIENTALIS.

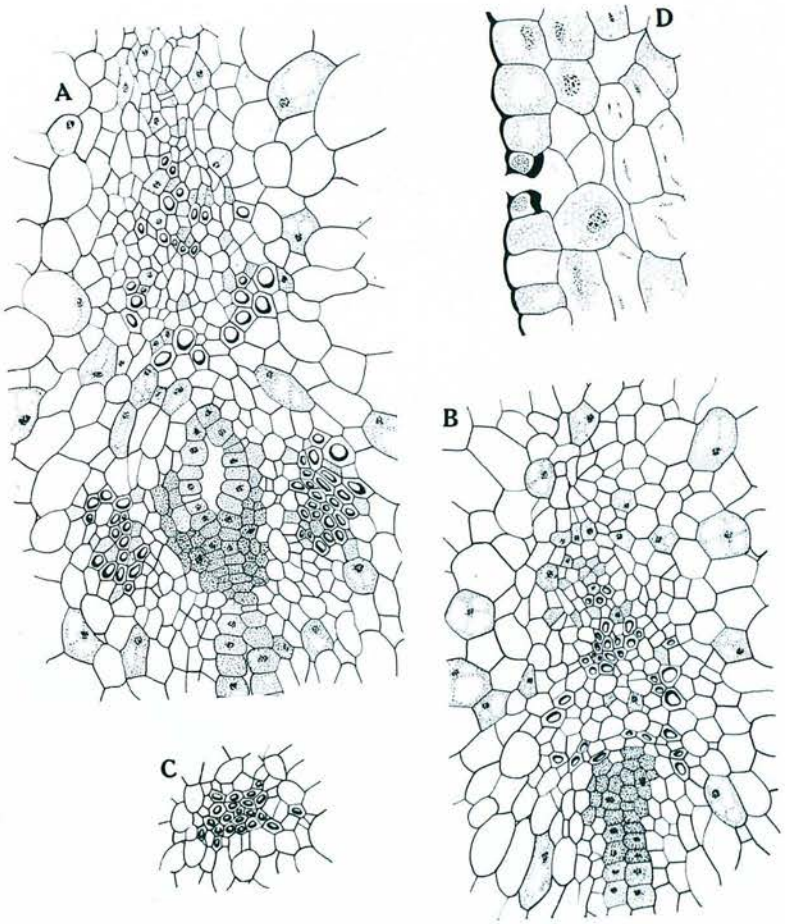
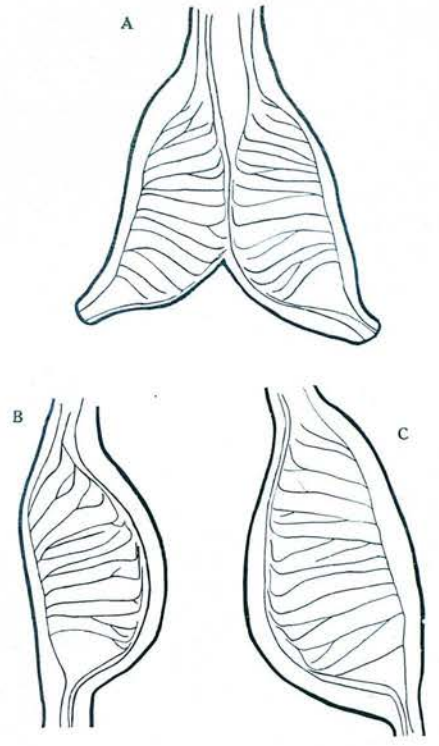


Fig. 25.



HELLEBORUS

ORIENTALIS.

Fig. 26.

HELLEBORUS

FOETIDUS.

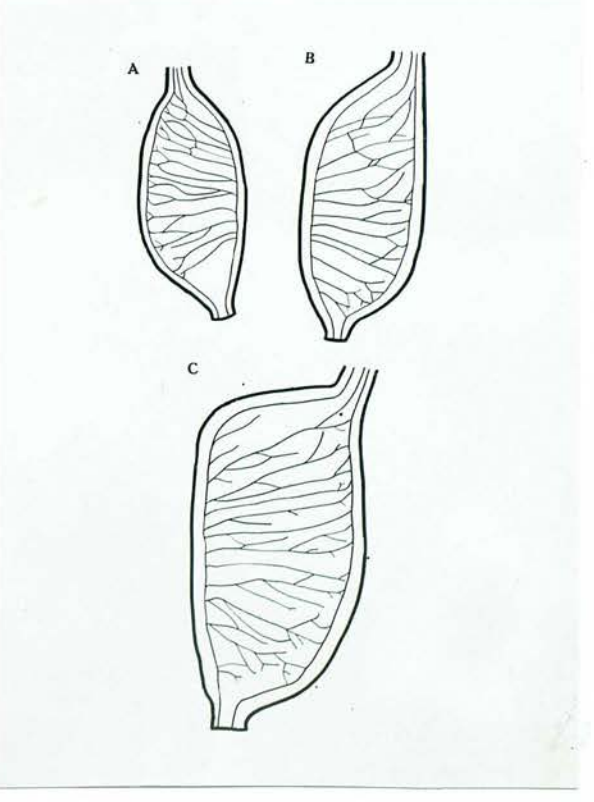


Fig. 27.

HELLEBORUS FOETIDUS.

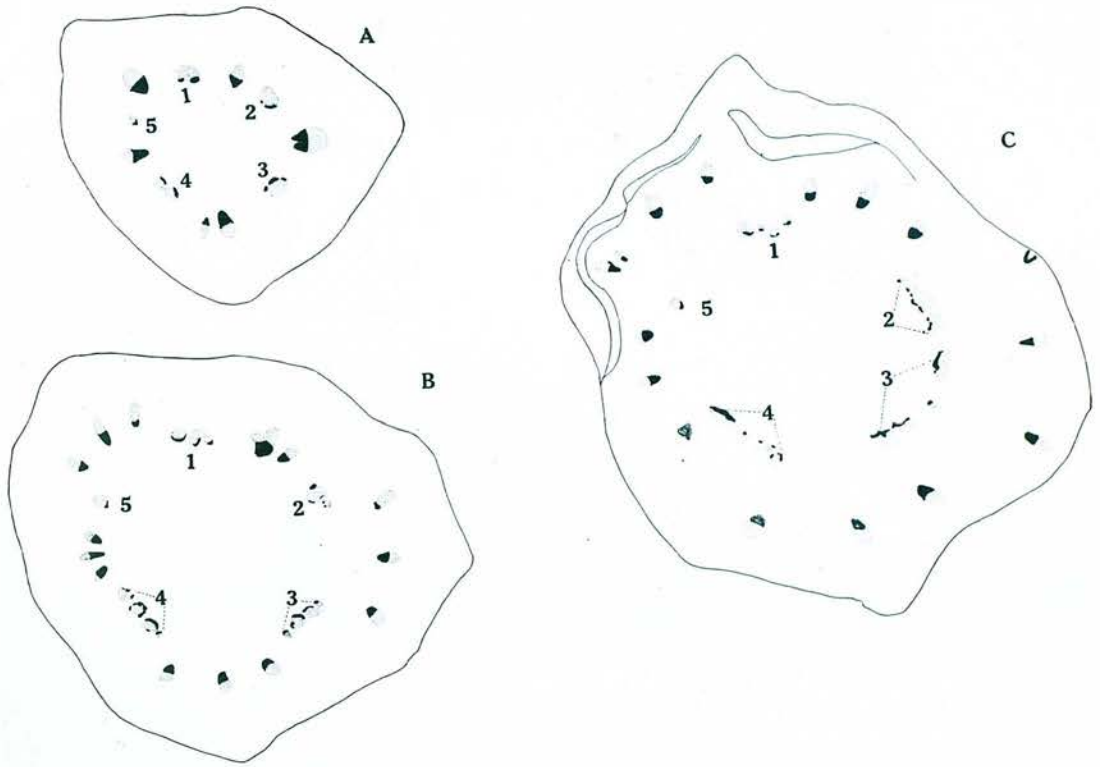


Fig. 28.

HELLEBORUS FOETIDUS.

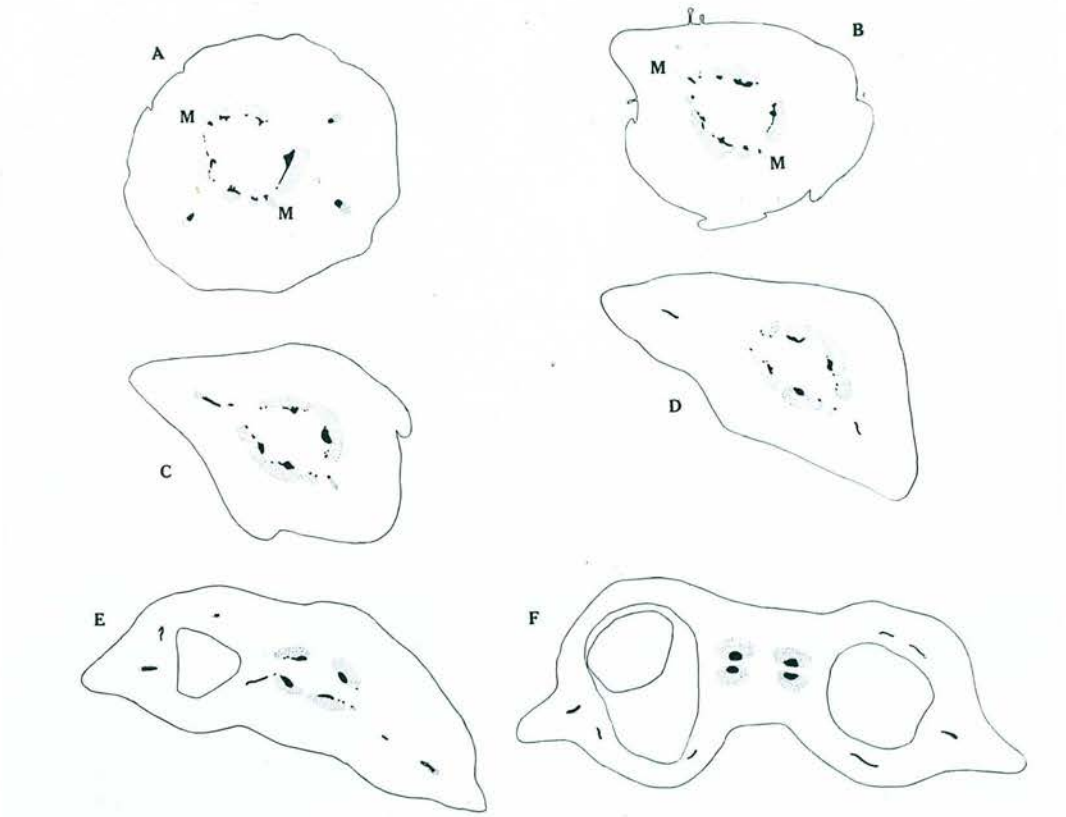


Fig. 29.

HELLEBORUS FOETIDUS.

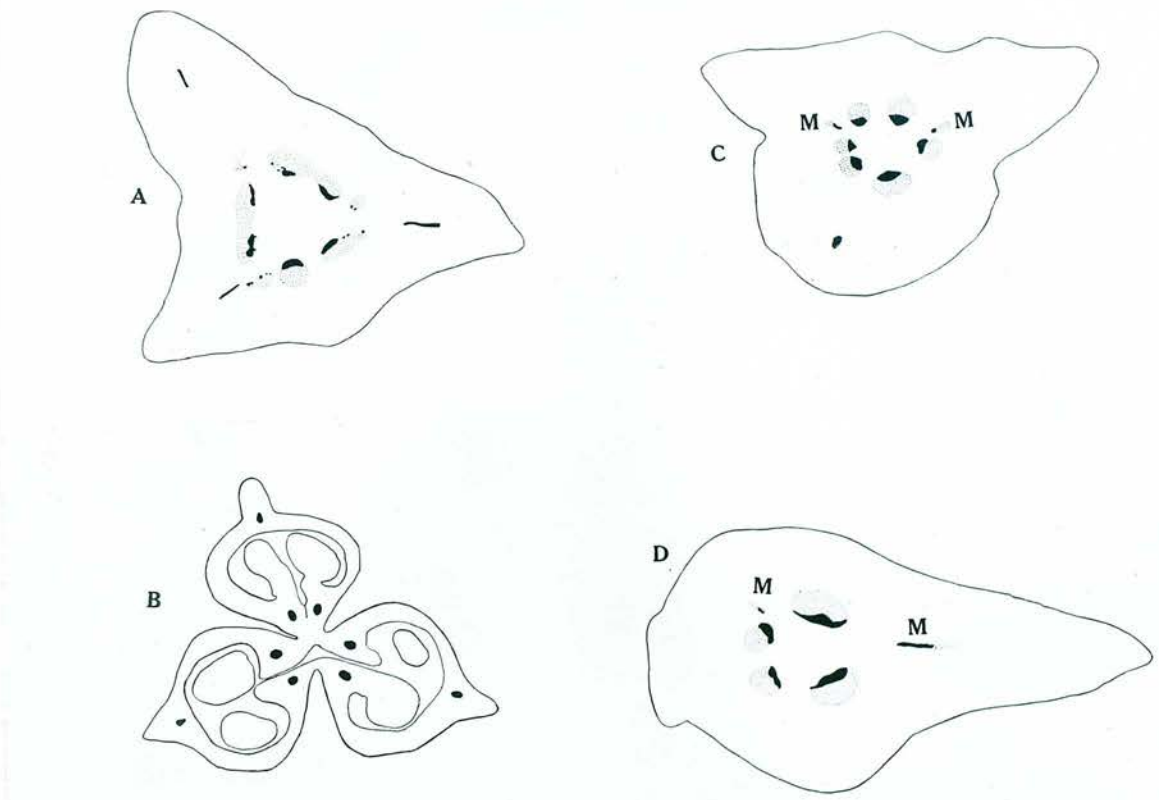


Fig. 30.

HELLEBORUS FOETIDUS.

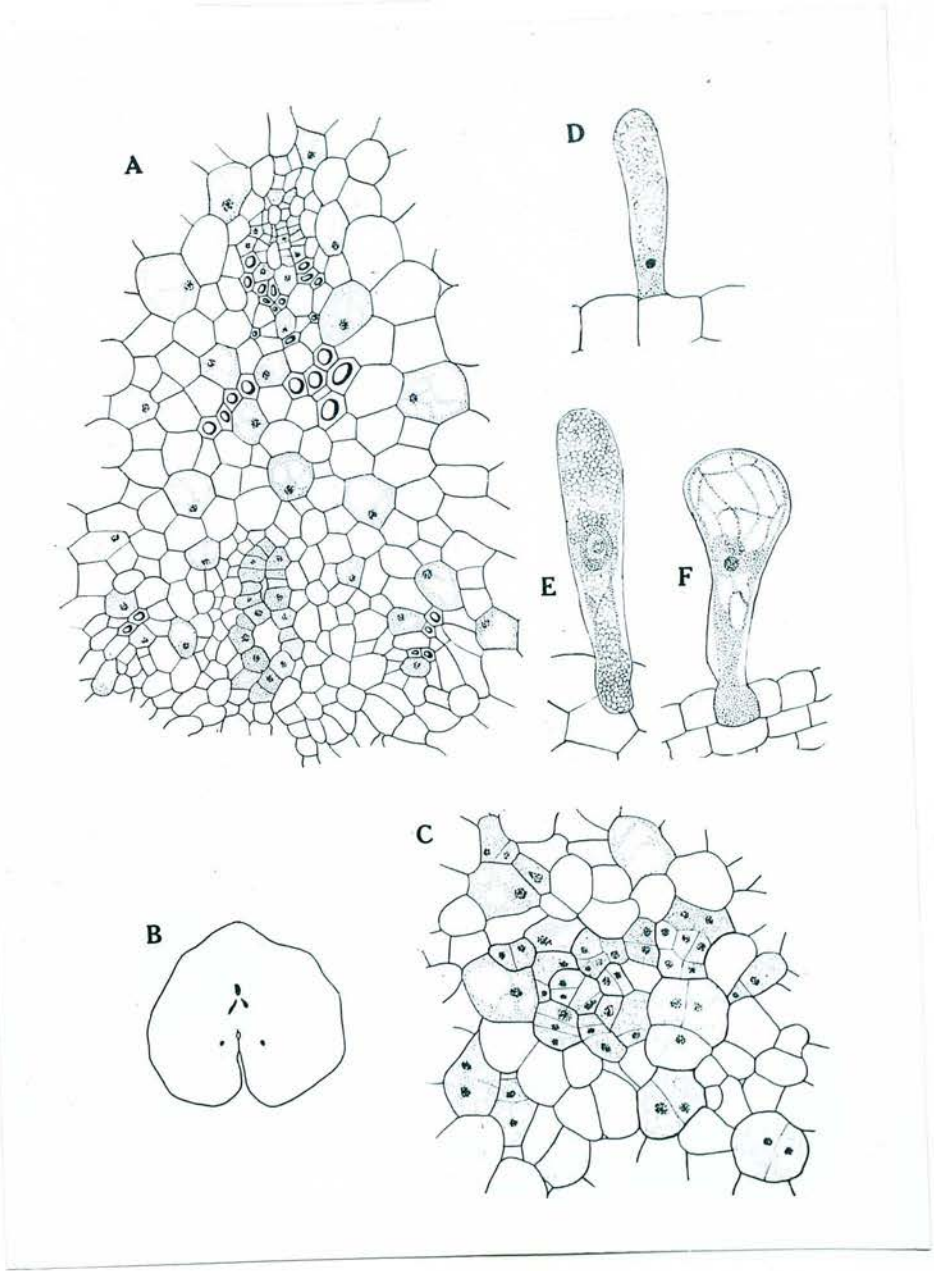


Fig. 31.

HELLEBORUS VIRIDIS.

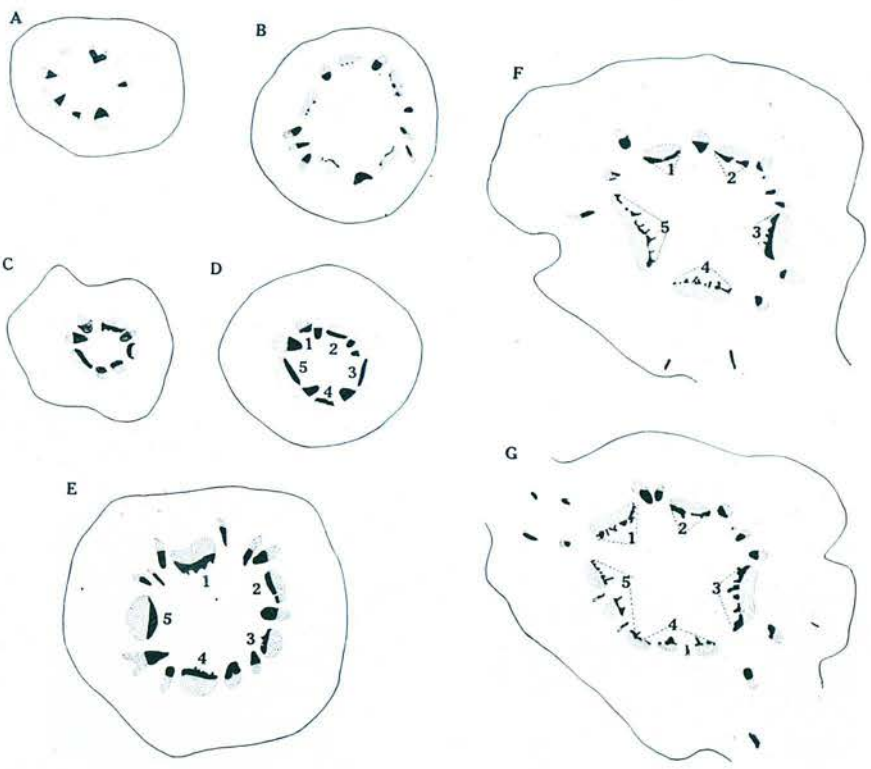


Fig. 32.

HELLEBORUS VIRIDIS.

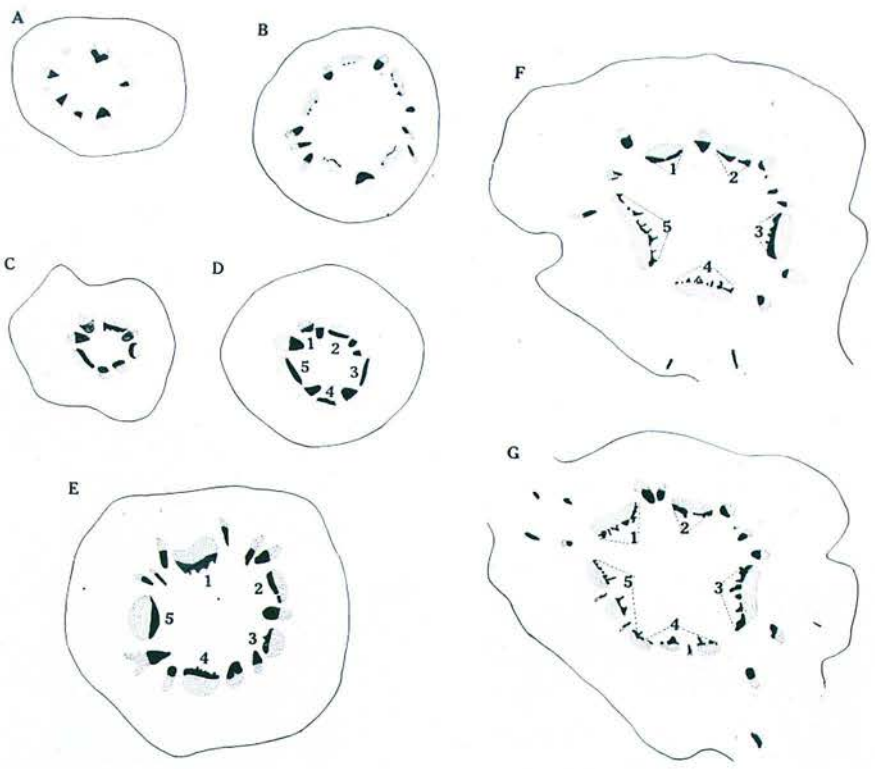


Fig. 32.

HELLEBORUS VIRIDIS.

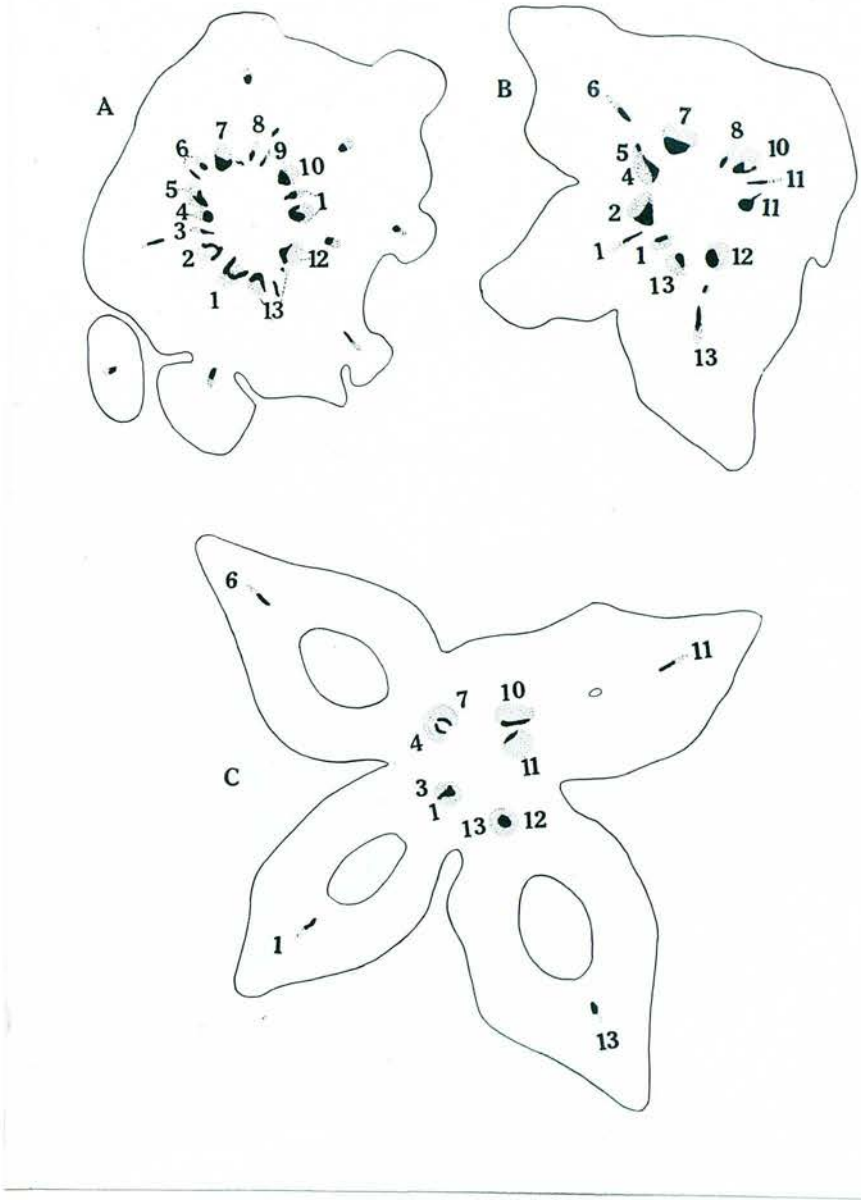


Fig. 33.

ERANTHIS CILICICA.

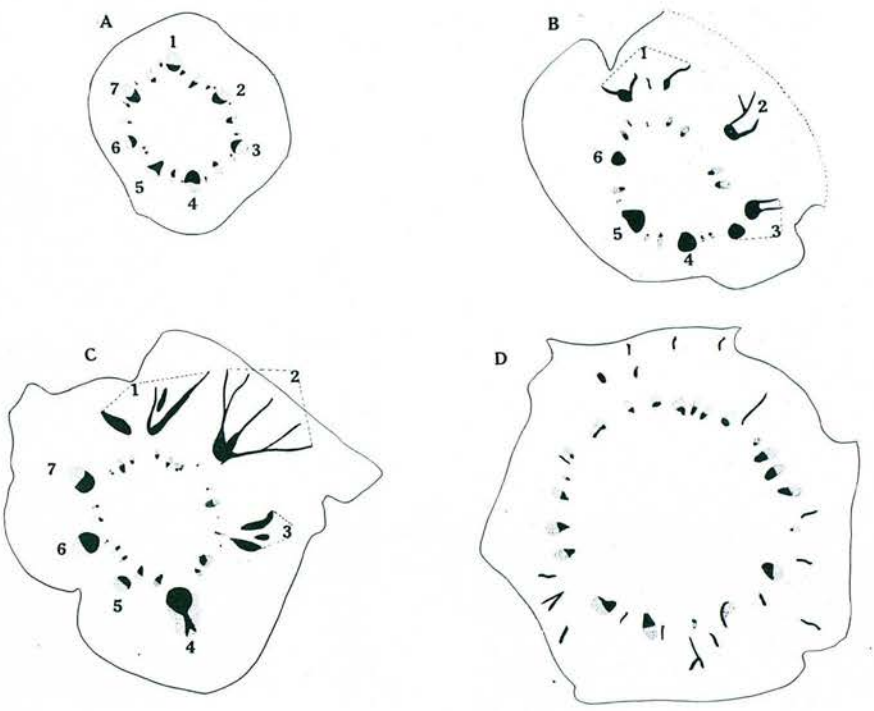


Fig. 34.

ERANTHIS CILICICA.

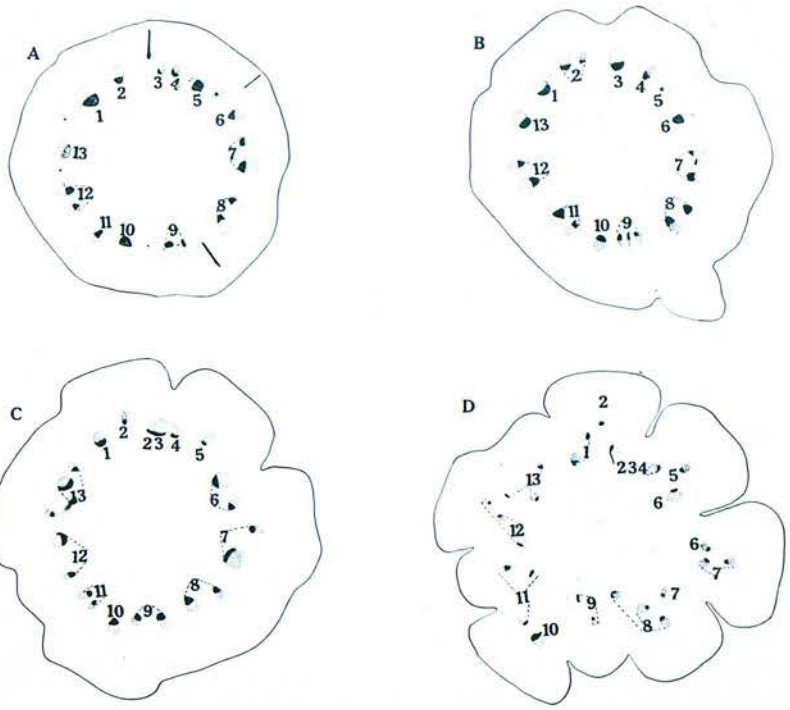


Fig. 35.

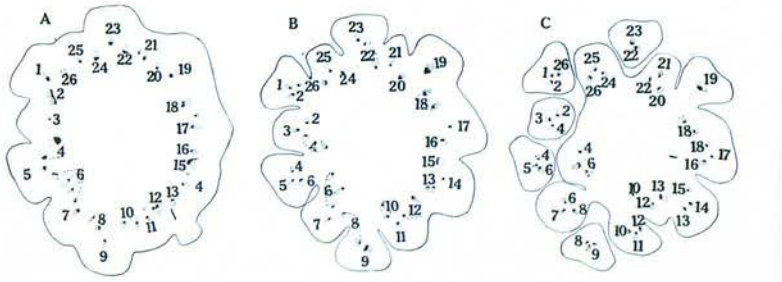


Fig. 36.

ERANTHIS CILICICA.

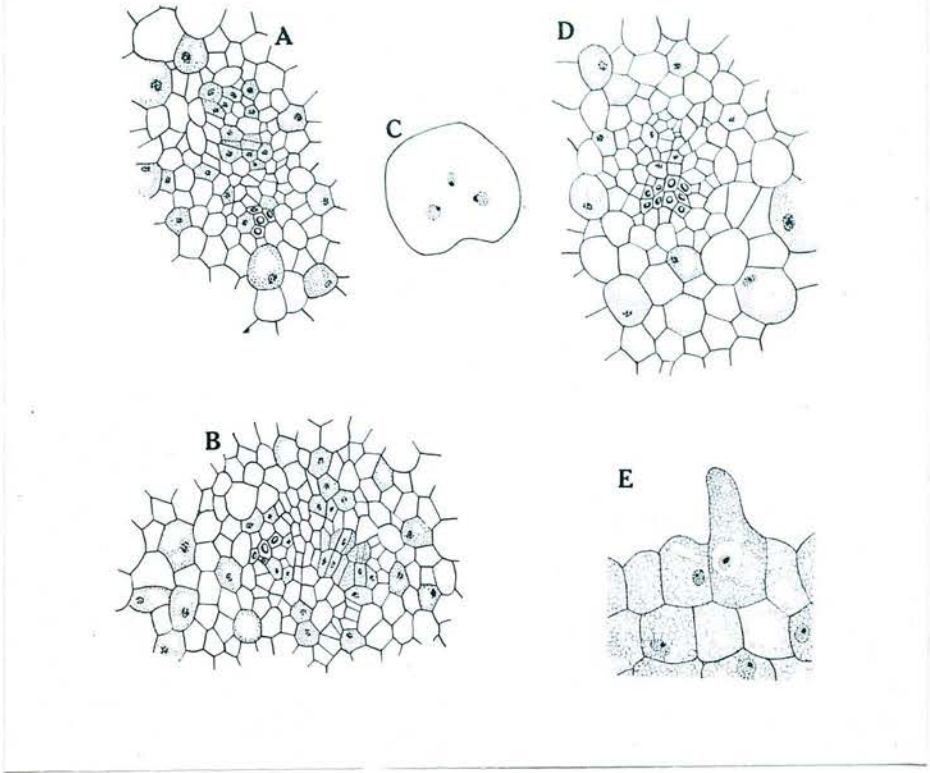


Fig. 37.

ERANTHIS HYEMALIS.

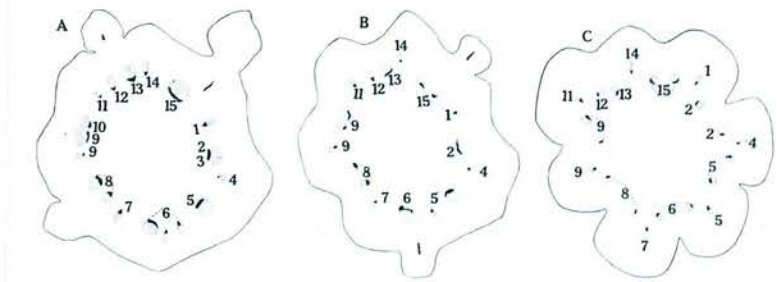
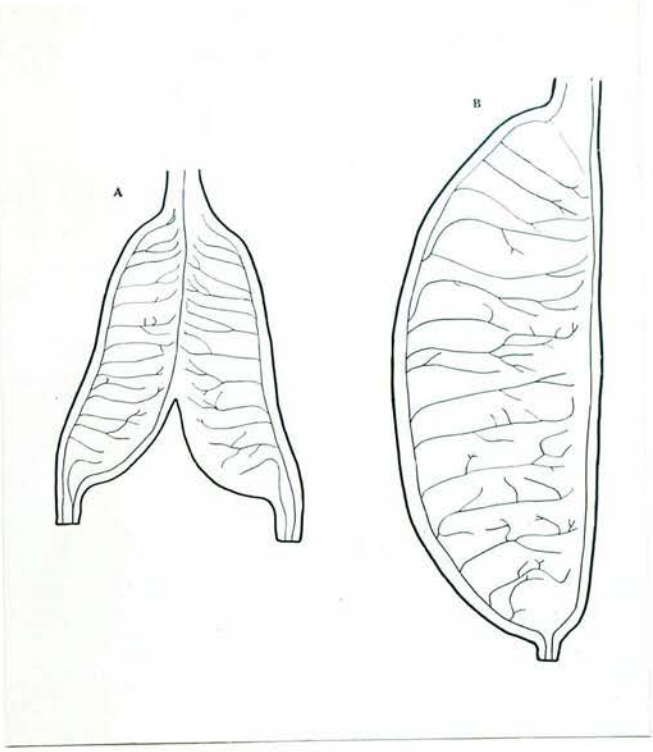
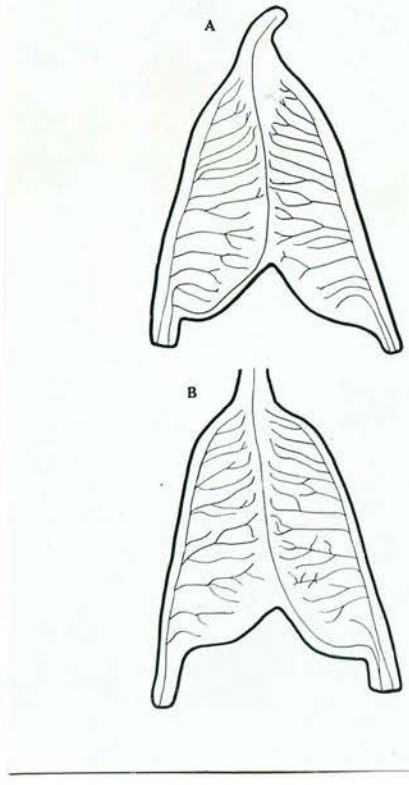


Fig. 38.



ERANTHIS CILICICA.

Fig. 39.



ERANTHIS HYEMALIS.

Fig. 40.

CIMICIFUGA DAVURICA.

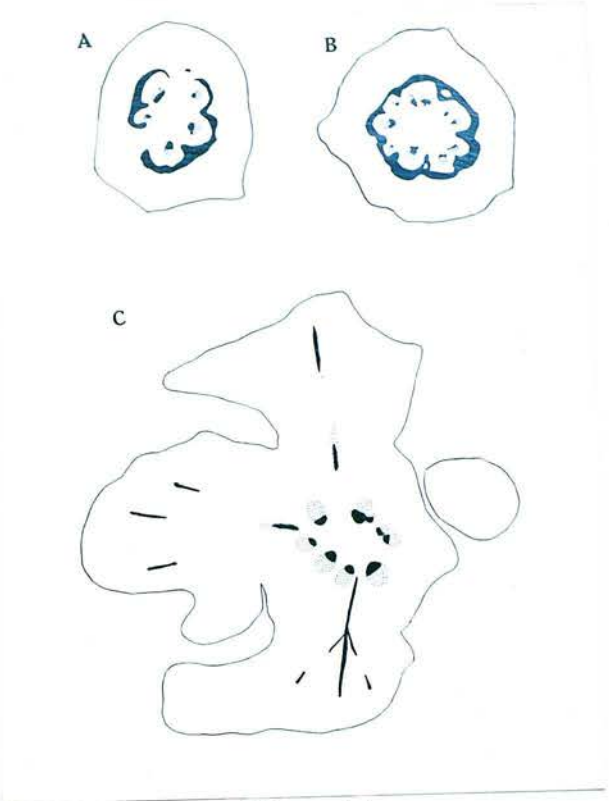


Fig. 41.

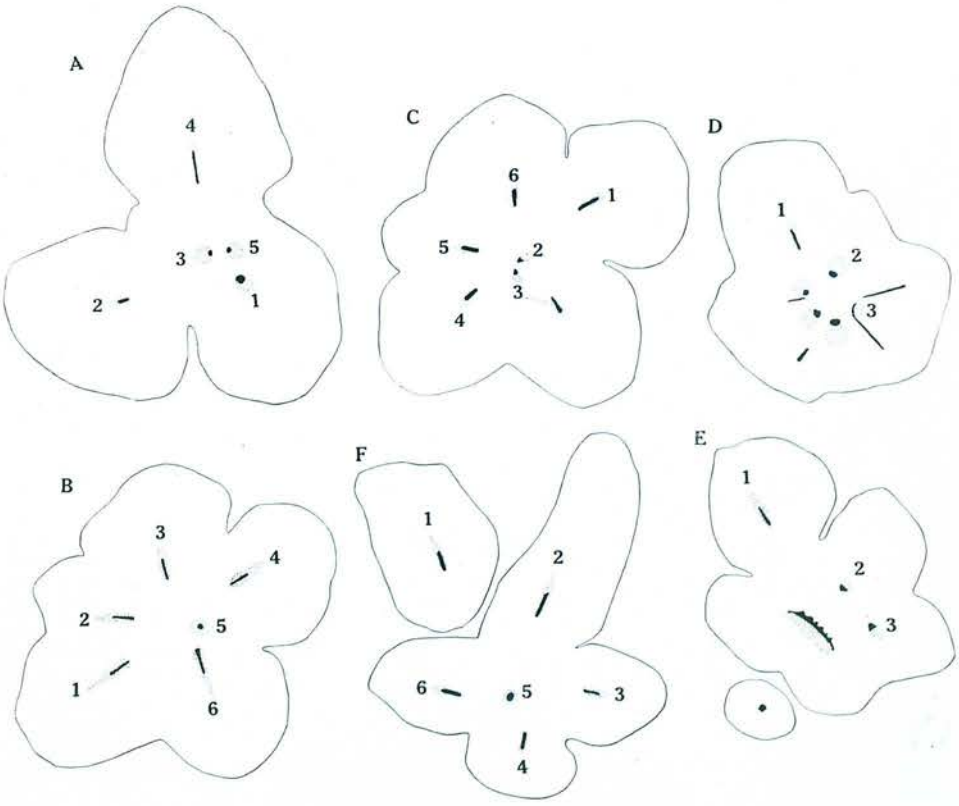


Fig. 42.

CIMIFUGA DAVURICA. CIMICIFUGA RACEMOSA.

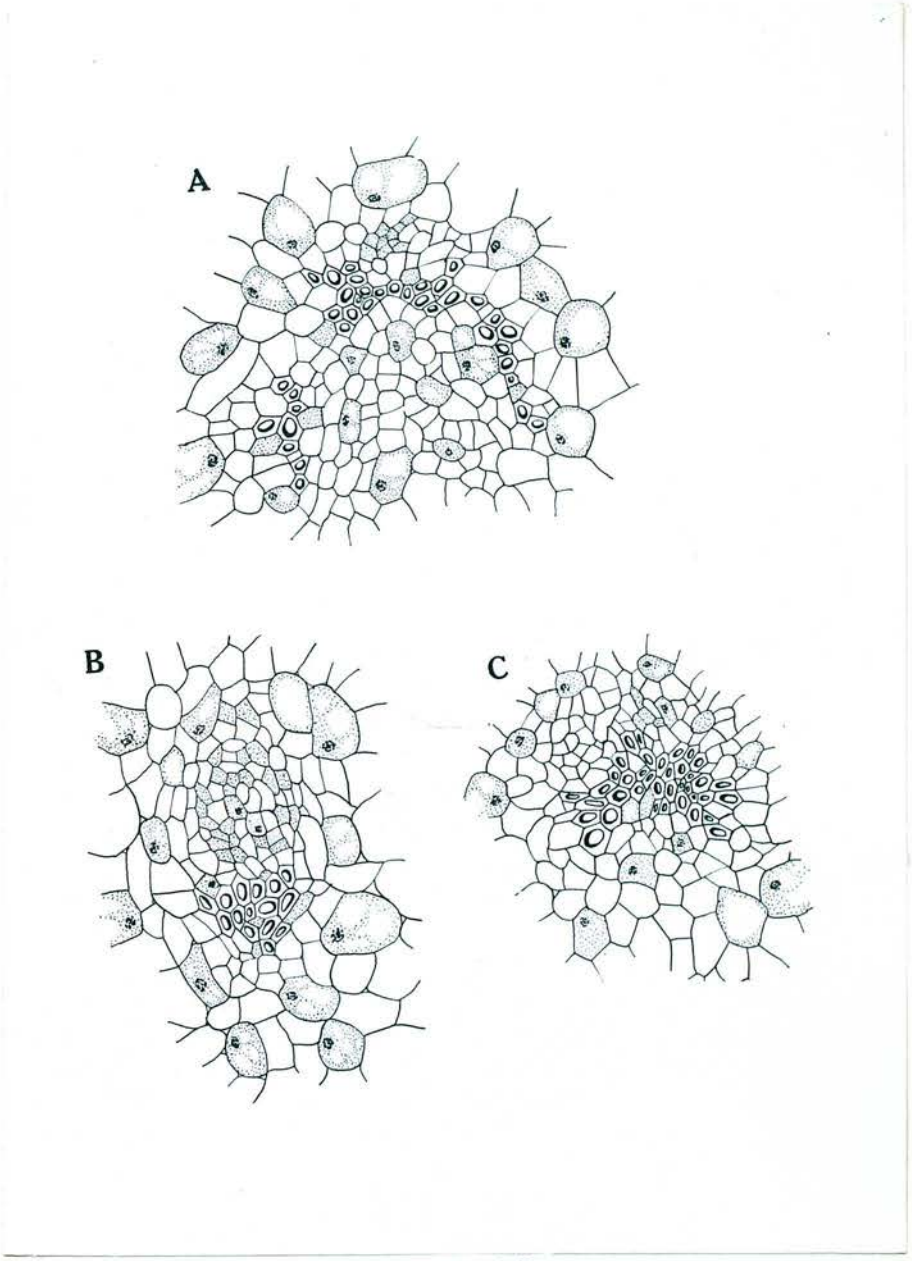


Fig. 43.

CIMIFUGA DAVURICA.

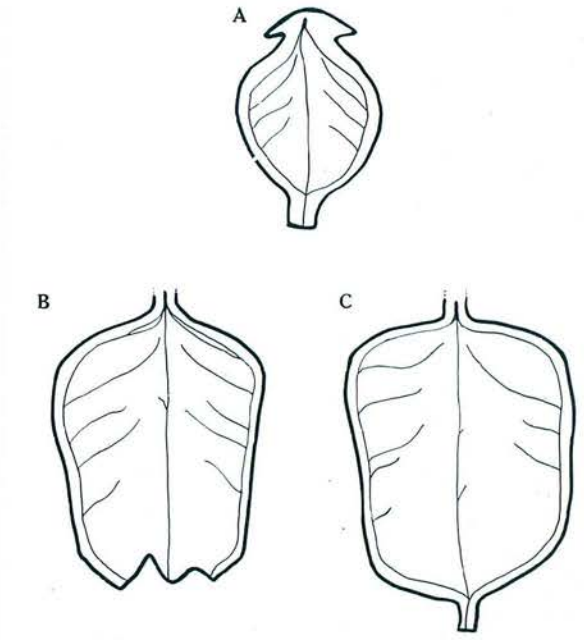


Fig. 44.

CIMIFUGA RACEMOSA.

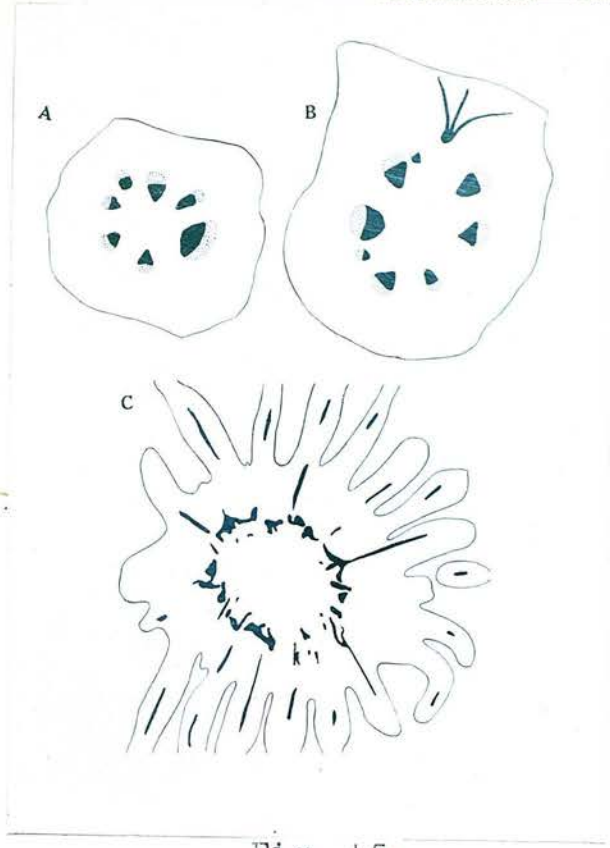


Fig. 45.

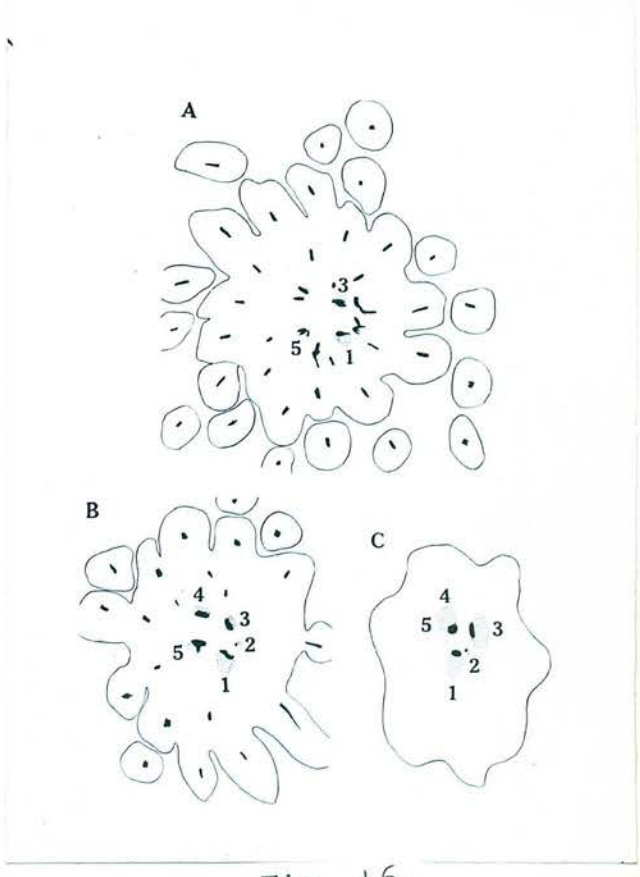


Fig. 46.

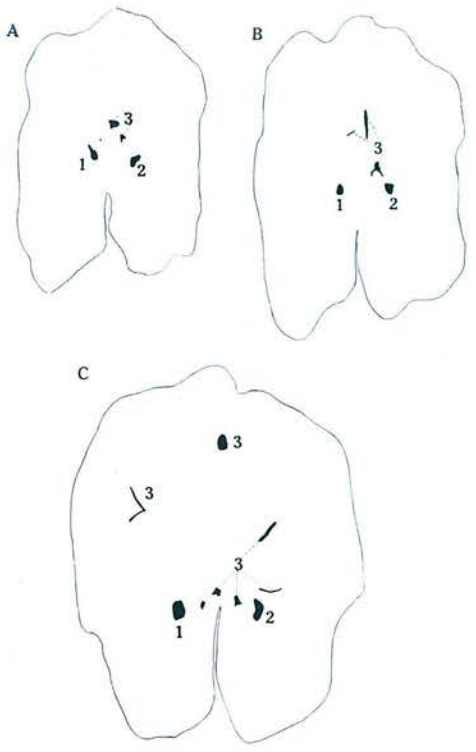


Fig. 47.

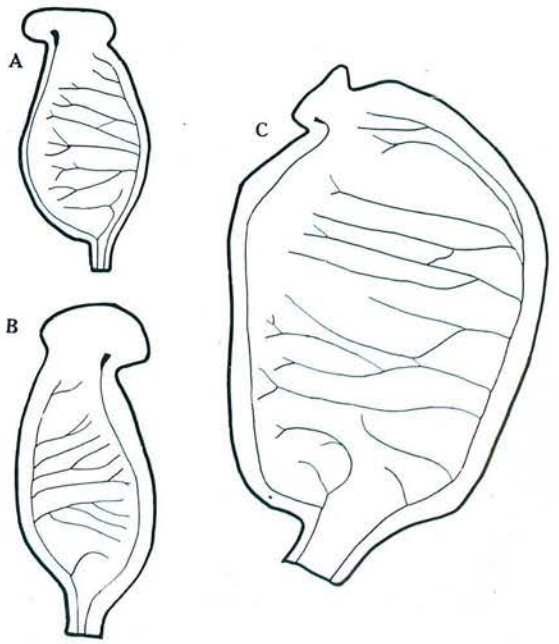


Fig. 48.

XANTHORHIZA APIIFOLIA.

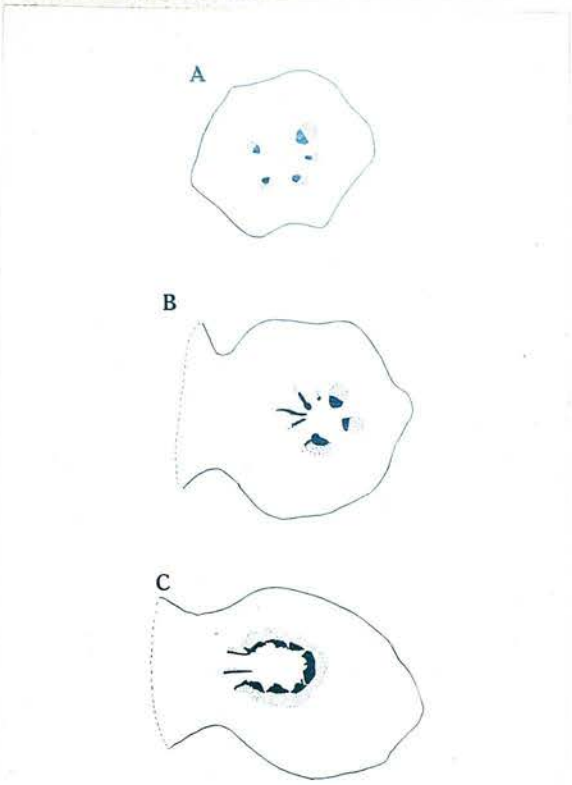


Fig. 49.

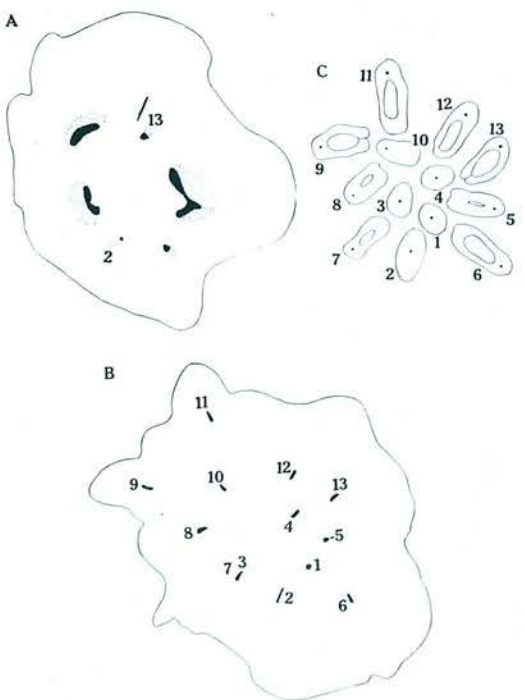
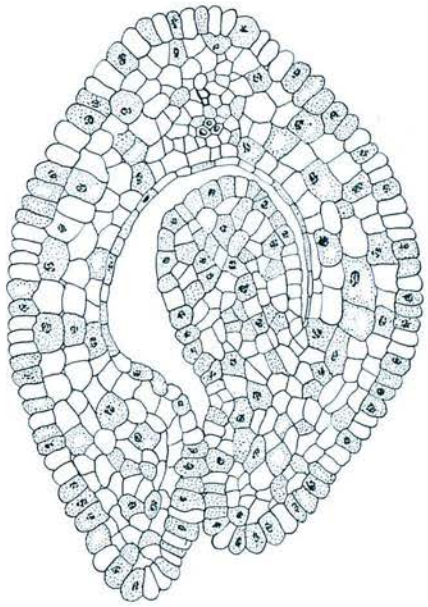


Fig. 50.

XANTHORHIZA APIIFOLIA.



Flg. 51.

TROLLIUS - GARDEN VARIETY.

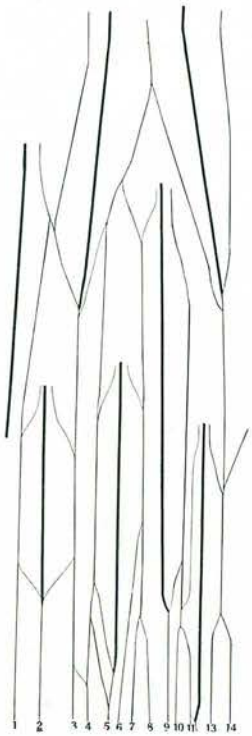


Diagram I.

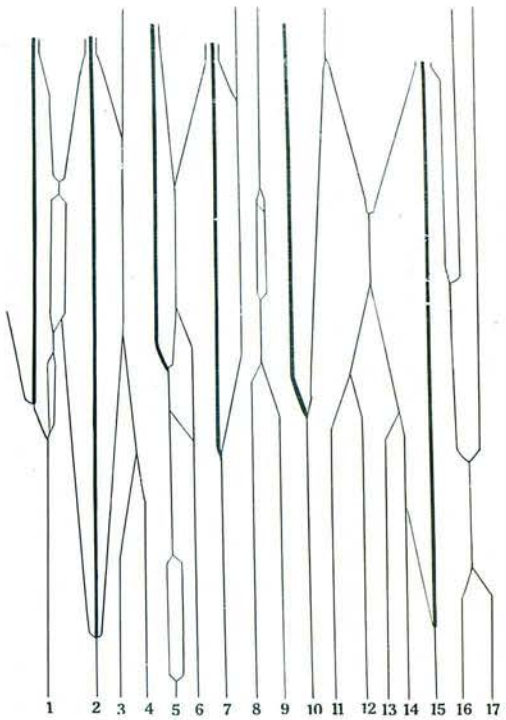


Diagram II.

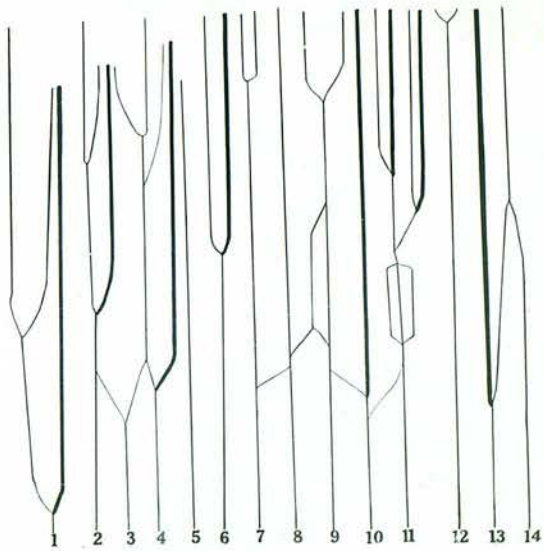


Diagram III.

CALTHA PALUSTRIS.

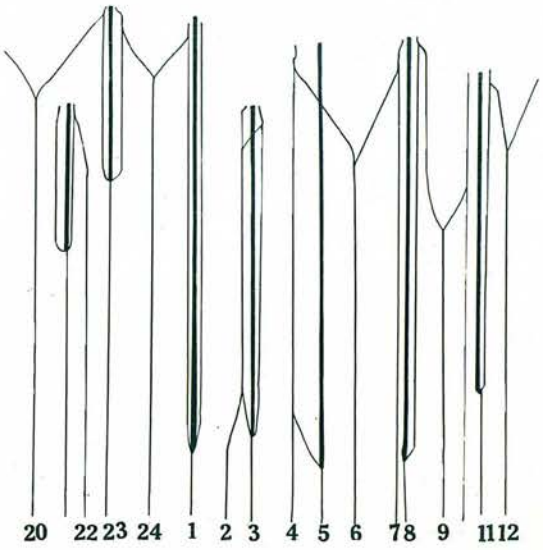


Diagram IV.

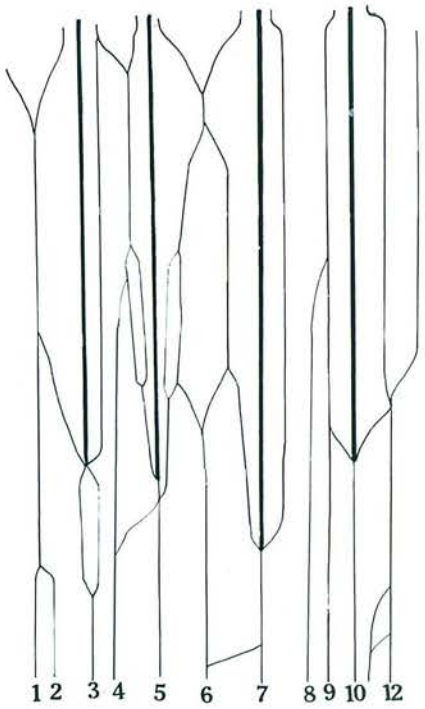


Diagram V.

CALTHA PALUSTRIS.

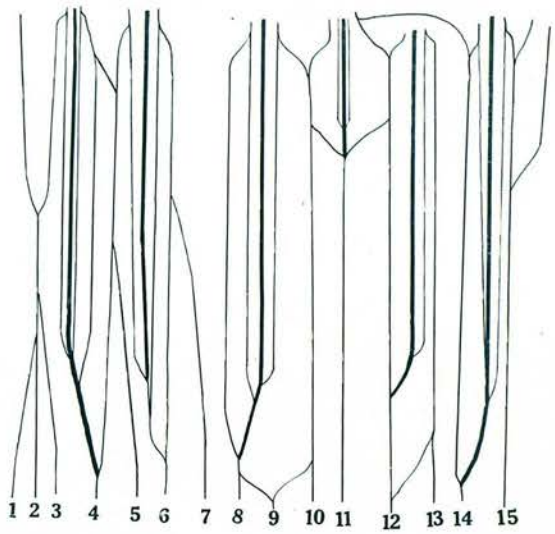


Diagram VI.

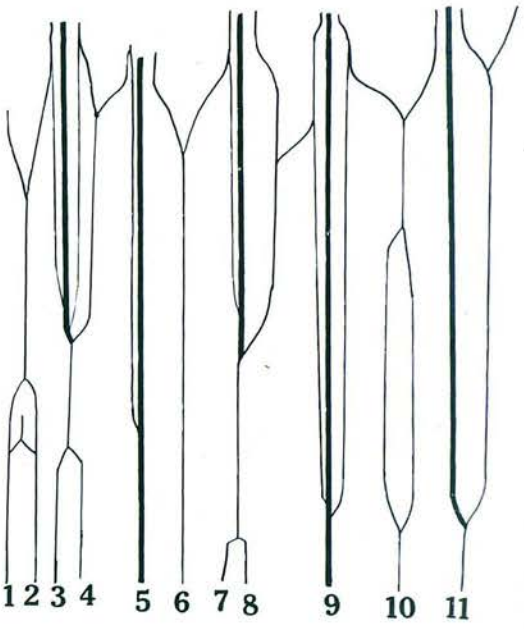


Diagram VII.

HELLEBOMUS ORIENTALIS.

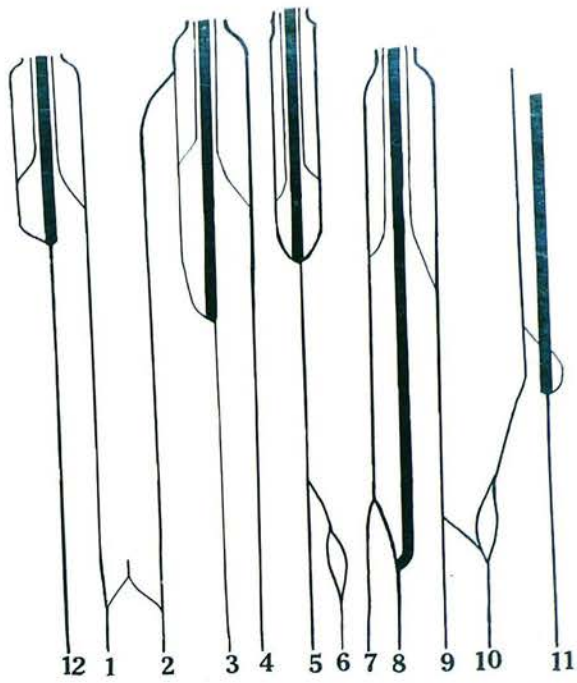


Diagram VIII.

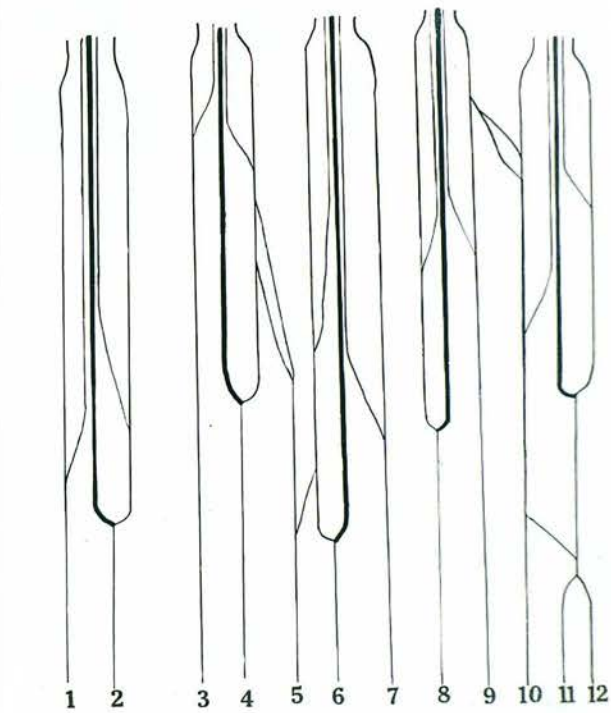


Diagram IX.

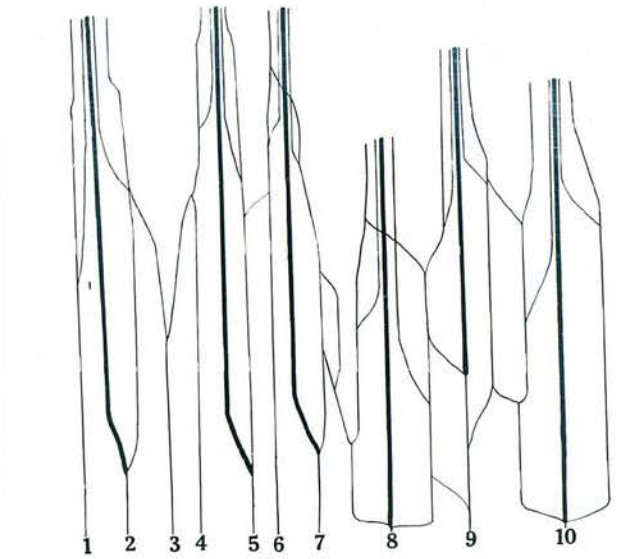


Diagram X.

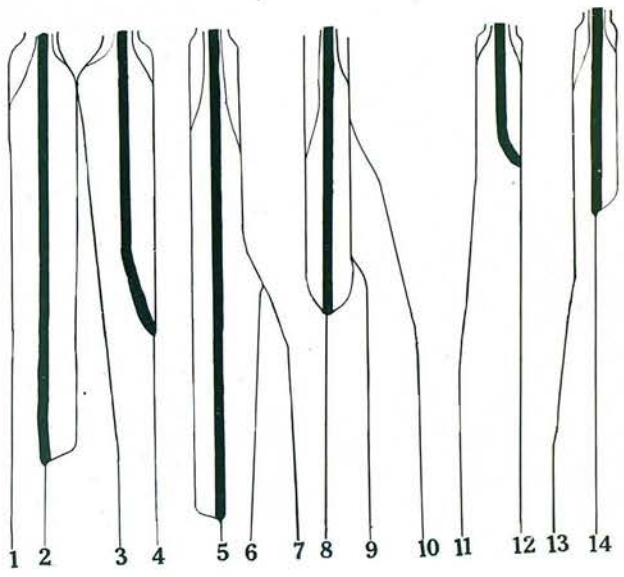


Diagram XI.

HELLEBORUS VIRIDIS.

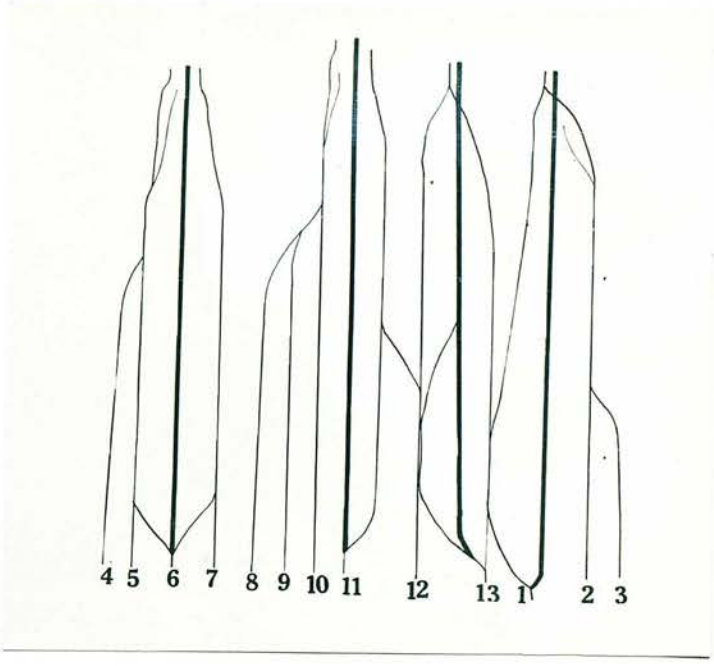


Diagram XII.

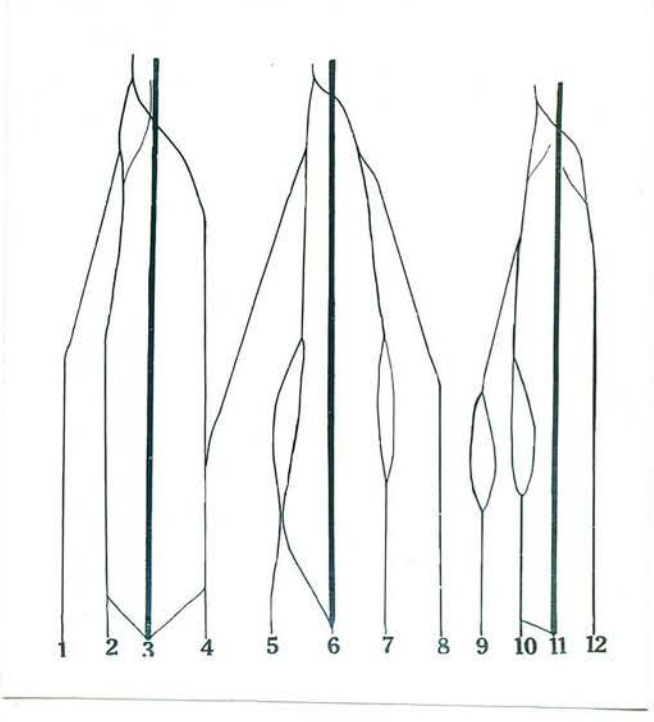


Diagram XIII.

ERANTHIS CILICICA.

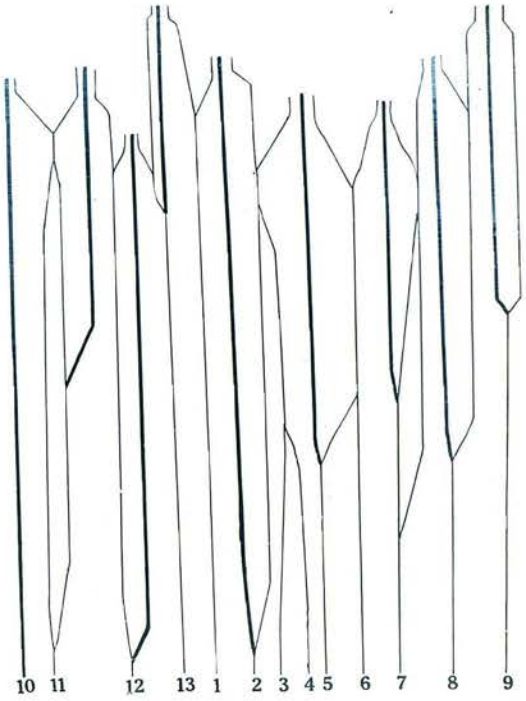


Diagram XIV.

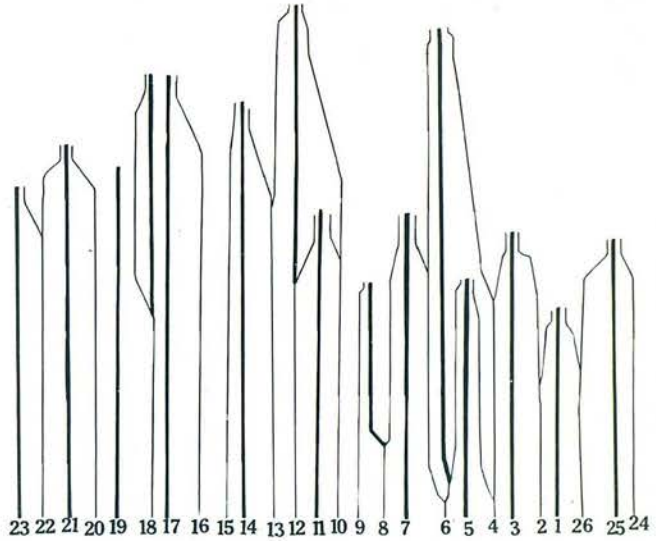
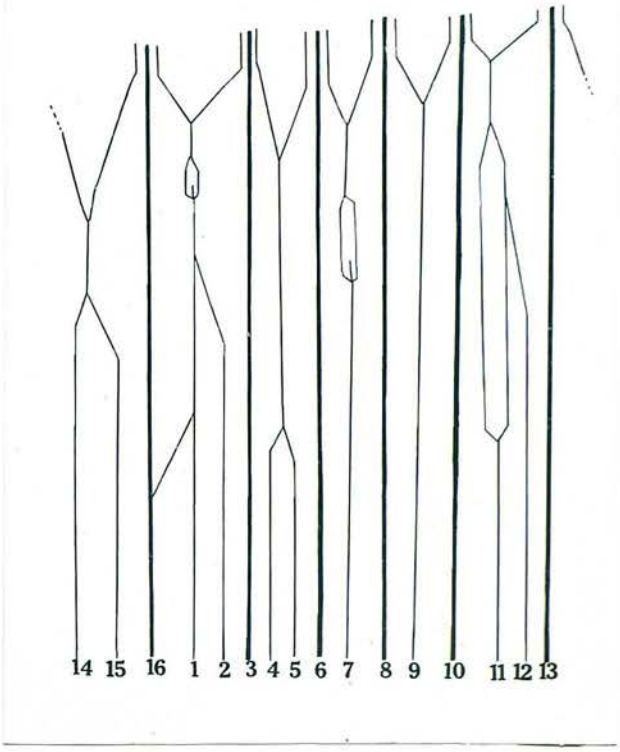


Diagram XV.

ERANTHIS HYEMALIS.



DiagramXVI

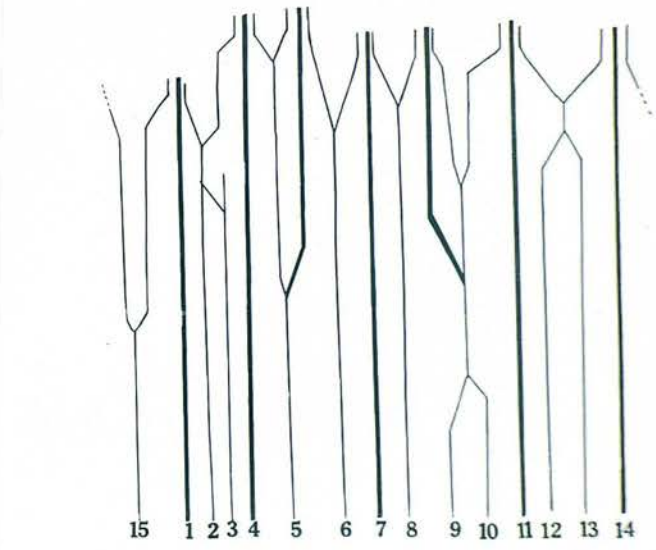


Diagram XVII.